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# Rhodora

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# RHODORA



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**Cover Illustration**

*Amelanchier nantucketensis* Bickn., the Nantucket Shadbush, is found only on dry moors, pine-barrens and pond margins on Nantucket and Martha's Vineyard Islands. A surculose, loosely colonial shrub to 2 m, this member of the Rosaceae is currently a candidate plant for federal listing. Original artwork by Alison Dibble.

Rhodora

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# *SCHIEDEELLA ROMEROANA* (ORCHIDACEAE, SPIRANTHINAE), A NEW AND INTERESTING SPECIES FROM MEXICO

DARIUSZ L. SZLACHETKO

## ABSTRACT

*Schiedeella romeroana* Szlach., *sp. nov.*, is newly described. It is distinguished by its lack of both rostellum and viscidium. The lip is distinctly divided into a rectangular hypochile with reduced basal auricles and a rounded epichile. It is compared with *S. valerioi* (Ames & Schweinf.) Szlach. & Scheviak, *S. amesiana* Garay and *S. llaveana* (Lindl.) Schlecht.

Key Words: *Schiedeella,* Orchidaceae, new species, Mexico

The genus *Schiedeella* Schlecht. embraces 10 species found in Mesoamerica—from the southern states of the U.S.A. to El Salvador and Costa Rica. The principal characteristics of these species are the structure of the flower segments and gynostemium. In the majority of these species the flowers are very small, with the lip set on a short, narrow claw, divided more or less distinctly into hypochile and epichile, with basal auricles of various size and shapes. The column foot is short and greatly reduced, the rostellum with a narrow base is linear-lanceolate, and after removing the semi-sheath-like viscidium it remains subulate with 1 or 3 indentations at the apex. Floral and cauline bracts are herbaceous (Szlachetko, 1992).

While conducting studies on the subtribe Spiranthinae for the Flora Mesoamericana, I found a new, distinctive plant among the herbarium material from the Mexican state of Oaxaca. It differs from those previously described in its total lack of both rostellum



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and viscidium. The middle stigma lobe, which usually becomes the rostellum in orchids, is here membranous and transparent. Together with the terminal edges of the clinandrium, it stretches between the fairly stiff, resilient protruberances of the lateral stigma lobes. It does not thus constitute a barrier for the pollen mass, nor does it prevent autogamy. In this new species of *Schiedeella,* the pollinia protrude distinctly above the thin middle lobe of the stigma.

**Schiedeella romeroana** Szlach., *sp. nov.* (Figure 1). Species *Schiedeellae llaveanae* et *S. valerioi* similis, sed ab omnibus congeneribus rostello et viscidio nullo iam diversa.

Roots 5, up to 4 cm long, about 1 cm in diameter, clustered, fleshy. Stem 3.5 dm tall, 4 mm in diameter at base and about 1 mm in diameter under inflorescence, delicate, erect, tinged reddish, sparsely glandular under and within inflorescence. Cauline bracts 9, herbaceous with hyaline margins, acute, the middle and upper shorter than internodes. Leaf single, petiolate; petiole about 4 cm long, narrow; blade 5 cm long, 2.5 cm wide, ovate-lanceolate, acute. Inflorescence 9 cm long, about 20-flowered, lax. Flowers horizontal, tiny. Floral bracts 6–7 mm long, ovate-lanceolate, acute, semi-transparent, herbaceous, with hyaline margins, 1-nerved. Ovary about 6 mm long, slightly twisted, sparsely glandular in the upper part. Dorsal sepal 5 mm long, 1 mm wide, oblong-lanceolate, obtuse, thin, semi-transparent, 1-nerved, sparsely glandular outside near the base. Lateral sepals 6 mm long, 1.3 mm wide, oblong, subobtuse, asymmetric, otherwise as the dorsal one. Petals 4.9 mm long, .6 mm wide, oblong-spathulate, obtuse, very thin, 1-nerved. Lip on short and narrow claw, divided into a hypochile and epichile; hypochile 4 mm long, 2.2 mm wide, rectangular, slightly thickened in the middle, the basal auricles rounded; epichile 2 mm long, 1.9 mm wide, rounded, minutely dentate, papillate, subobtuse. Gynostemium 3.5 mm long, slender, slightly arcuate, lacking rostellum and viscidium. Anther about 1 mm long, ovate-cordate. Pollinia with attenuate apices and rounded bases.

TYPE. Mexico. Oaxaca: km 6.3 from Ixtlan, on brecha N from km 5.8 on Natividad road, elev. 2100–2400 m. Bosque de pino y encino, con *Arbutus.* In shade, in bud, flower and unripe capsule.

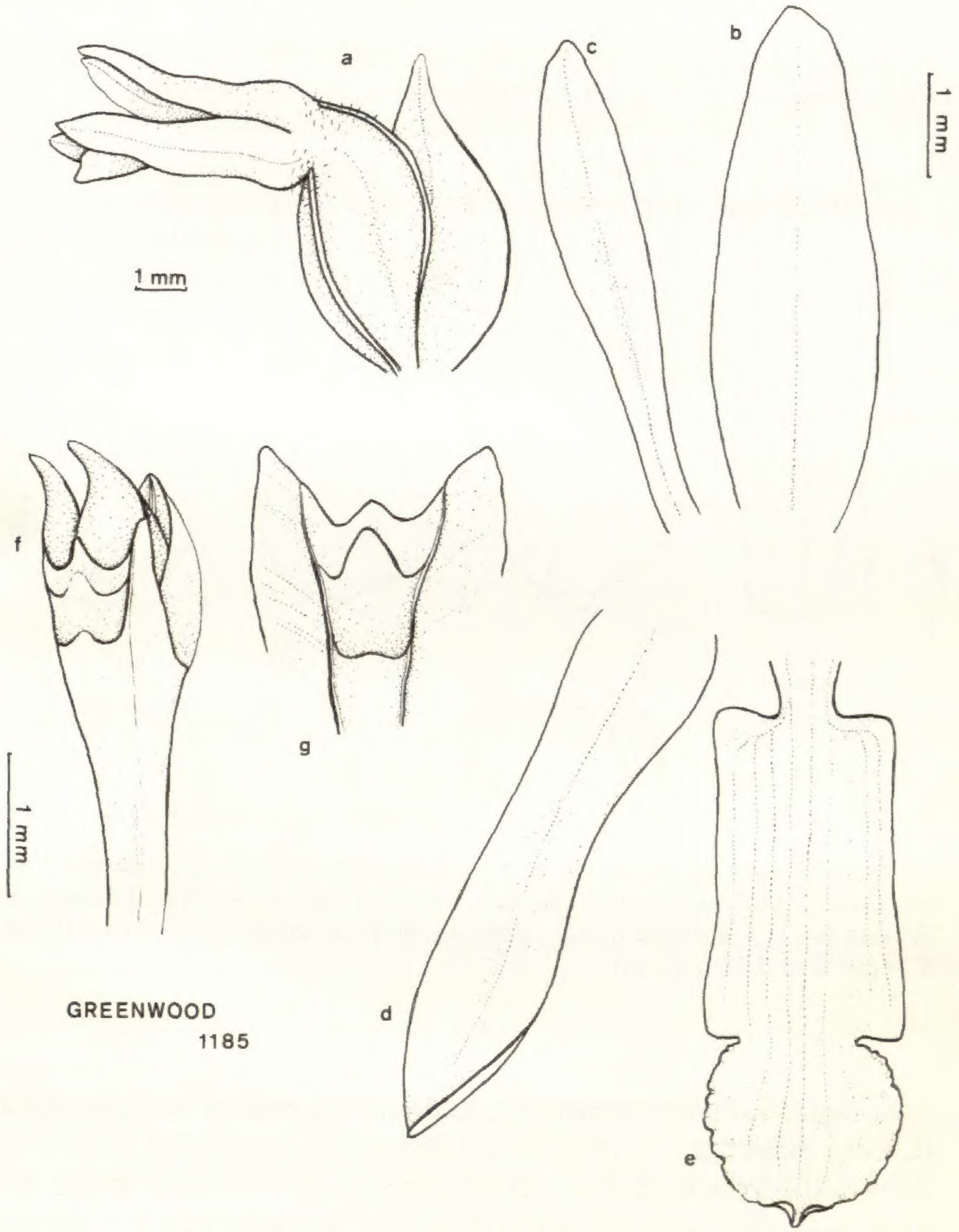


Figure 1. *Schiedeella romeroana* Szlach. **a.** flower and floral bract. **b.** dorsal sepal. **c.** petal. **d.** lateral sepal. **e.** lip. **f.** gynostemium. **g.** stigma.

Very few spikes seen, ca. 10, versus ca. 200 leaves in October 1983. 18 Mar 1984. *Greenwood 1185* (HOLOTYPE: AMO).

ETYMOLOGY. I dedicate this species to Dr. Gustavo A. Romero, Curator of the Oakes Ames Orchid Herbarium, Harvard University, in gratitude for his invaluable help in my work on the revision of the subtribe Spiranthinae.

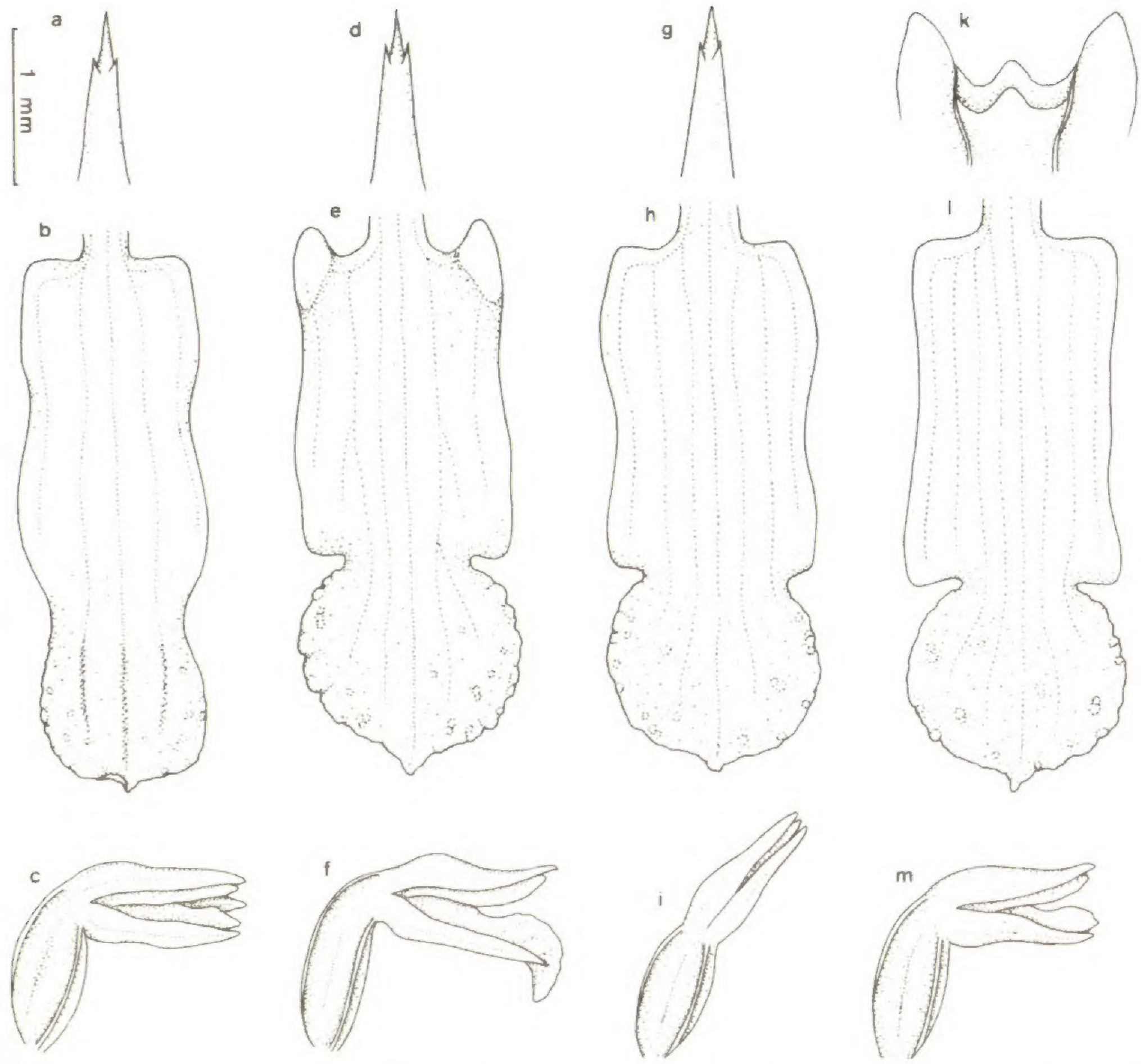


Figure 2. Comparison of the rostellum remnant (above), lip form (middle) and flower (below) between *Schiedeella valerioi* (Ames & Schweinf.) Szlach. & Sheviak (**a–c**), *S. llaveana* (Lindl.) Schlecht. (**d–f**), *S. amesiana* Garay (**g–i**) and *S. romeroana* Szlach. (**k–m**).

*Schiedeella romeroana* seems to be closely related to *S. llaveana* (Lindl.) Schlecht., *S. amesiana* Garay and *S. valerioi* (Ames & Schweinf.) Szlach. & Sheviak (Figure 2). It is similar in the lip form to the first species and to the last in the proportion of length of lip to remaining perianth segments. It has horizontal flowers instead of the erect flowers of *S. amesiana.*

ACKNOWLEDGMENTS

I am grateful to Prof. Dr. Hab. Ryszard Ochyra for translation of the Latin diagnosis, and the Curator of AMO for loan of herbarium materials.

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# *SARRACENIA PURPUREA* L. SSP. *VENOSA* (RAF.) WHERRY VAR. *BURKII* SCHNELL (SARRACENIACEAE)—A NEW VARIETY OF THE GULF COASTAL PLAIN

DONALD E. SCHNELL

**ABSTRACT**

A new variety of *Sarracenia purpurea* L. ssp. *venosa* (Raf.) Wherry is herein described as var. *burkii.* The variety is confined to the Gulf coastal plain and is characterized by pale pink to lavender petals and a white to pale green-white carpel, the umbraculate portion of the style being most apparent in this respect.

Key Words: *Sarracenia purpurea* ssp. *venosa, Sarracenia purpurea* ssp. *venosa* var. *burkii,* Gulf coastal plain, southeastern U.S.

*Sarracenia purpurea* L. ssp. *venosa* (Raf.) Wherry is a carnivorous pitcher plant found mainly in the coastal plain of the southeastern United States, with mountain extensions in the Carolinas. There is a gap in its range in southern Georgia, and populations occur again in the central Gulf coastal plain (Wherry, 1933; McDaniel, 1966; Schnell, 1976). The Gulf coastal populations are addressed in this paper.

In 1933, Edgar Wherry (p. 4) commented on what he described as a "mutant" of *Sarracenia purpurea* with an almost white umbraculate portion of the style and pale rose-pink petals, collected near Theodore, Alabama by Frank Morton Jones in 1910. Wherry found additional plants in 1932 (he did not specify exactly where, but implied southern Alabama) and sent them to Louis Burk of Philadelphia, an apparently well-regarded horticulturist of the day. The plants flowered true to the original description in Burk's greenhouse the following year. Wherry (1933) suggested the possibility of naming a horticultural variety in honor of Mr. Burk, but never did.

Over a period of thirty-five years of botanizing the *Sarracenia* range, I have examined characters of North American pitcher plants in a series of papers (Schnell, 1978a, 1978b, 1979, 1981) in which *S. purpurea* ssp. *venosa* in the central Gulf coastal plain was mentioned. Gradually, I became impressed with the fact that nearly all specimens of the subspecies were similar to those described by Wherry; rather than being a rare mutant, it is essentially the only form present. The floral characters described, their con-

Figure 1. *Sarracenia purpurea* ssp. *venosa* var. *burkii* in flower, growing in the open. Sepals are a deep red while the widely paduriform petals are pale pink.

Figure 2. *Sarracenia purpurea* ssp. *venosa* var. *burkii.* Note nearly white umbraculate portion of the style. Light colored petals are pink to lavender in this example.

sistency among populations, and partial isolation because of the southern Georgia "gap" indicate sufficient circumscription to designate a variety of the subspecies.

**Sarracenia purpurea** L. ssp. **venosa** (Raf.) Wherry var. **burkii** Schnell, *var. nov.*

Petalis pallide roseis vel lavandulaceis, stylis umbraculatis ovariisque albis vel pallide subviridulis, et sepalis diverse viridirubris vel purpurascentibus praediti.

Petals pale pink or lavender, umbraculate style and ovary white to very pale green, sepals variably green-red to purple.

TYPE LOCALITY. United States. Alabama. Washington County, off U.S. 45 near Deer Park: Open seep bog. 4 April 1992. (HOLOTYPE: NCU, pressed plants and color photos.)

ETYMOLOGY. Named after early twentieth century horticulturist Louis Burk since Dr. Wherry expressed interest in honoring Mr. Burk.

Figure 3. *Sarracenia purpurea* ssp. *venosa* var. *burkii*. In this example, the ovary and inferior portion of the style are nearly white, while the umbraculate portion is green-white.

RANGE. Central Gulf coastal plain: Florida panhandle from Liberty County west through the lower quarter of Alabama and Mississippi.

HABITAT. Open or moderately shaded pine savannas, seep bogs and along slow, shallow meandering streams. Common among other *Sarracenia* spp.

Plants grown in my greenhouse and outdoors clearly indicate that these characters are fixed and contrast markedly with the red to maroon petals and green (occasionally suffused with red) carpels of Atlantic coastal and mountain populations of ssp. *venosa*.

Interestingly, plants growing with maximum sun exposure have the palest carpels (almost pure white), while more shaded plants tend to have some very pale green in the carpel. Petal color does not vary with light exposure, and sepals do vary in depth of color.

*Sarracenia purpurea* ssp. *venosa* var. *burkii* grows often in large dense populations composed of many species of the genus, and all these individuals tend to hybridize readily one with the other, with many backcrosses in evidence. Care should be exercised

when the occasional plant of *S. purpurea* with red or maroon petals and green carpels is found. Given the fecundity of Sarracenias in this range, one might reasonably speculate that such plants may be the product of hybridization with back-crossing and possible macrorecombination.

Selfing of plants of var. *burkii* under greenhouse conditions results in abundant seedset and greater than 95% germination with typical adult plants as the eventual outcome.

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# *RHODODENDRON ALBIFLORUM* HOOK. (ERICACEAE): ONE TAXON OR TWO?

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## ABSTRACT

Populations of *Rhododendron albiflorum* Hook. in Colorado are disjunct by ca. 1470 km from populations in the Pacific Northwest. Morphological data showed that plants from the two sets of populations differed in length and width of petals and length of stamens. Genetic identity figures based on analysis of isozyme electrophoresis found Colorado and Pacific Northwest populations to have an $\bar{I}$ value of .76. These morphological, geographical and isozymic data support recognition of the Colorado plants as *Rhododendron albiflorum* Hook. var. *warrenii* (A. Nelson) M. A. Lane, *comb. & stat. nov.*; the Pacific Northwest plants are *Rhododendron albiflorum* Hook. var. *albiflorum*.

Key Words: *Rhododendron albiflorum*, morphology, isozyme electrophoresis, disjunct populations, Colorado, Pacific Northwest.

## INTRODUCTION

*Rhododendron albiflorum* Hook. ("Cascades Azalea" or "White Rhododendron") is a small shrub of subalpine areas in the Cascade Mountains of northern California and Oregon, the Olympic Mountains of Washington, and the Rocky Mountains of British Columbia, Alberta and Montana, with disjunct (by ca. 1470 km) populations in the Rocky Mountains of Routt and Jackson Counties, Colorado (Figure 1). The plants have grayish bark and short-petiolate, narrowly elliptic, sparingly pubescent leaves. White flowers are borne in small axillary clusters; corollas are broadly campanulate and up to 2 cm wide. Though the plants are very attractive, they are extremely difficult to cultivate, and so the species is not well known among azalea fanciers.

Named by Hooker (1838), *Rhododendron albiflorum* is based on a specimen from "alpine woods of the Rocky Mountains" collected by Drummond, probably in Alberta or southeastern British Columbia during his journey there in 1825–27 (McKelvey, 1956). In 1900, Rydberg included Hooker's plant in *Rhododen-*

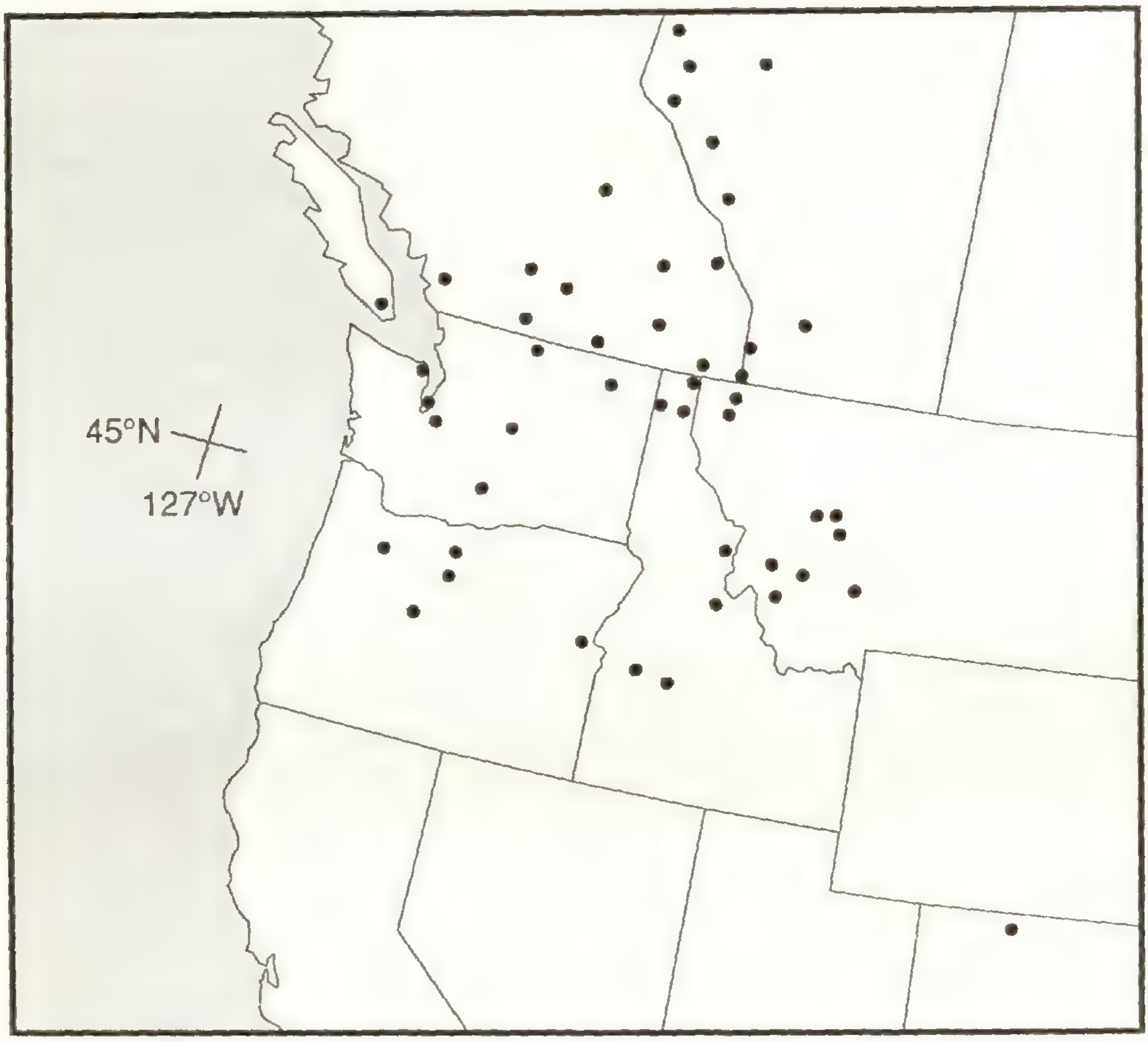


Figure 1. Distribution of *Rhododendron albiflorum* Hook. Each dot may represent one or more collections. The Colorado populations (Three Island Lake, Lake Diana, Lake Katherine, Lone Pine Creek, Gilpin Lake, Ute Pass and Slavonia) all lie within a 50 sq. mi. area in the Mount Zirkel Wilderness Area of Routt National Forest in Routt and Jackson Counties, Colorado.

*dron* subg. *Azaleastrum,* and elevated the subgenus to generic status. He contended that the deciduous leaves of *Azaleastrum albiflorum* (Hook.) Rydberg distinguished it from *Rhododendron,* and that its large sepals, lateral flowers, peltate stigmas and campanulate corollas separated it from *Rhodora* and *Azalea.* Nelson (1913) accepted Rydberg's generic treatment of the Pacific Northwest plants, but considered the Colorado populations sufficiently different to warrant specific status, and named them *Azaleastrum warrenii* A. Nelson. Most authors of floras (e.g., Harrington, 1954; Peck, 1961; Hitchcock and Cronquist, 1973) have accepted neither Rydberg's genus nor Nelson's species, though Weber (1990) and Weber and Wittmann (1992) use *A. albiflorum* (Hook.) Rydberg for the Colorado populations. A recent monographic treat-

ment (Philipson and Philipson, 1986) considered *R. albiflorum* to be the sole member of *Rhododendron* subg. *Candidastrum*, which nonetheless clusters with sect. *Azaleastrum* of subg. *Azaleastrum* in phenetic analyses (Palser et al., 1991).

In this study, we asked two questions: 1. Do the populations from the Pacific Northwest and those from Colorado constitute one taxon or two? 2. If there is more than one taxon present, should they both be recognized at the species level, or both as varieties of a single species? We addressed these questions using morphometric and isozyme electrophoretic techniques.

## MATERIALS AND METHODS

Collection data obtained from a total of 712 specimens borrowed from 11 herbaria were used to construct a distribution map for the taxon (Figure 1). Pollen from a selection of these specimens was studied using both light and scanning electron microscopy. Eight quantitative characters, referred to below as variables five through twelve (VAR5 = leaf length, VAR6 = leaf width, VAR7 = number of flowers per cluster, VAR8 = sepal length, VAR9 = sepal width, VAR10 = petal length, VAR11 = petal width, and VAR12 = stamen length), were measured on representative specimens from the Pacific Northwest ($n$ = 51) and from Colorado ($n$ = 7). Variables one through four were geographic and specimen identifiers. Statistical analysis of these characters was carried out on a Macintosh IIsi microcomputer using SPSS for the Macintosh (SPSS, Inc., 1990).

Field observations and collection of leaf tissue for isozyme electrophoresis were carried out in the following localities (population acronym and number of individuals in parentheses): Colorado: Routt County, Routt National Forest, Mount Zirkel Wilderness Area, Three Island Lake (TIL, 20 individuals); Oregon: Marion Co., Mount Hood National Forest, Breitenbush Lake Road (BLR, 40 individuals); Washington: Clallam County, Olympic National Park, Hurricane Hill trailhead (ONP, 20 individuals); and British Columbia: Vancouver Island, Grouse Mountain Resort (GMR, 40 individuals). Voucher specimens were deposited at COLO and KANU.

Leaf samples in individual plastic bags were transported to the laboratory on wet ice, ground in buffer as described by Mitton et al. (1979), and stored at −80°C in microfuge tubes until use.

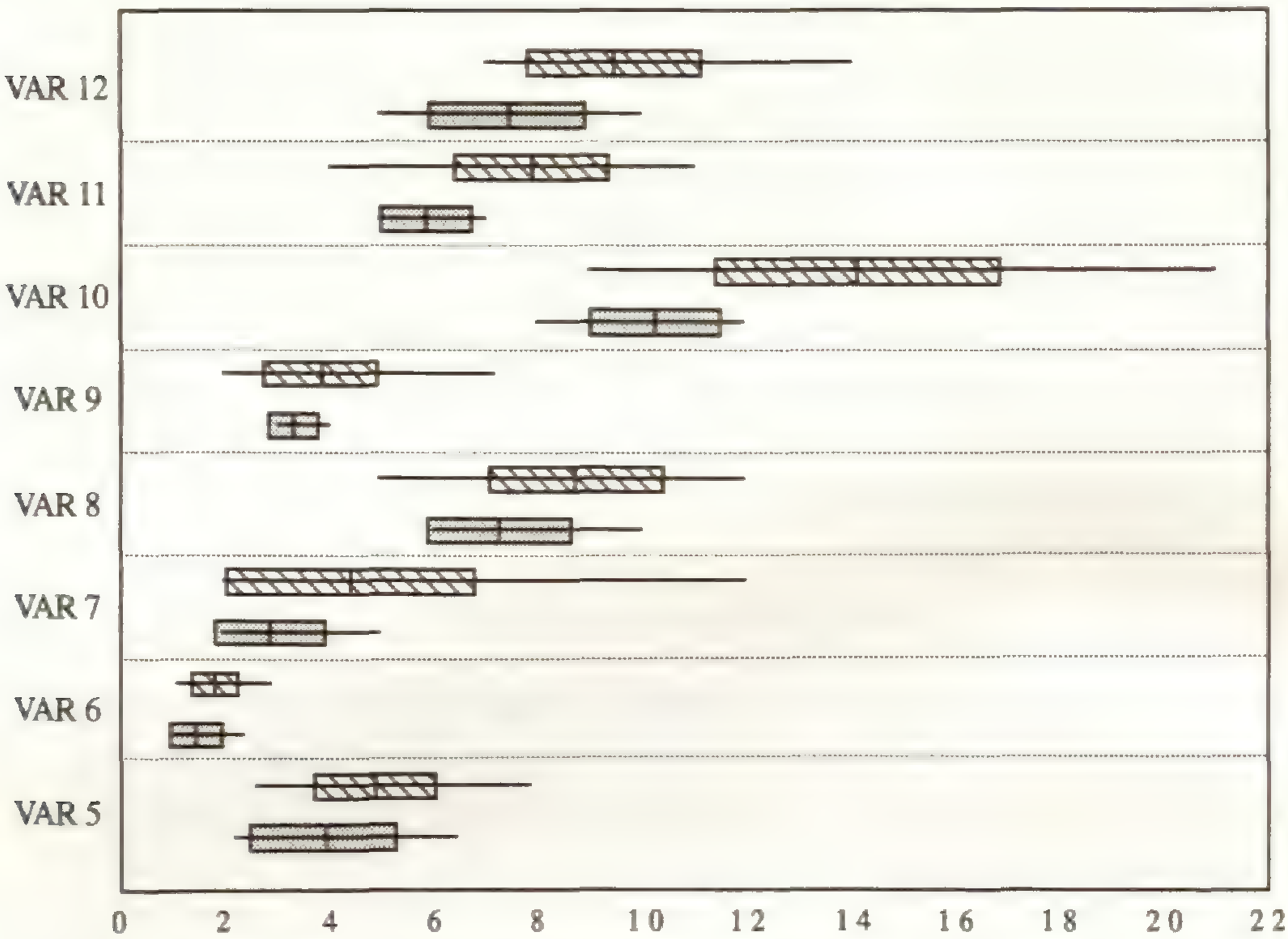


Figure 2. Graphic representation of the statistical analysis of eight meristic characters (*see* Materials and Methods for explanation) of *Rhododendron albiflorum* specimens from the Pacific Northwest ($n = 57$) and Colorado ($n = 7$). Numbers on x-axis are cm for variables 5–6 and mm for variables 7–12. Thin line = range, boxed area = mean ± one standard deviation (hatched fill = Pacific Northwest, solid fill = Colorado), vertical bar = mean. Note that while the means for some characters (e.g., petal length, VAR10, and petal width, VAR11) are significantly different (Table 1), the range for the Colorado populations is included within (VAR11) or greatly overlaps (VAR10) that of the Pacific Northwest populations, reducing their usefulness as taxonomic characters.

Starch gels were prepared according to protocols of Soltis et al. (1983). Interpretable banding patterns were obtained from the enzymes glucose-6-phosphate isomerase, phosphoglucomutase, leucine amino peptidase, aspartate amino transferase and triose-phosphate isomerase when run in buffer system 6 or a modification of buffer system 8 (Haufler, 1985). The clearest banding patterns for isocitric dehydrogenase, shikimate dehydrogenase, malate dehydrogenase, and 6-phosphogluconate dehydrogenase were obtained using buffer system 11 of Soltis et al. (1983) or a pH 7.5 modification of the morpholine system of Odrzykoski and Gottlieb (1984). Data from banding patterns were analyzed using the program BIOSYS-1 (Swofford and Selander, 1981) on a Zenith 159 microcomputer.

Table 1. Comparison of means and standard deviations (SD) for eight measured characteristics (VAR5 through VAR12, as explained in text) of Colorado and Pacific Northwest (Oregon, Washington, British Columbia, Alberta, Montana and Idaho) specimens of *Rhododendron albiflorum*. Measurements were taken from herbarium sheets; flowers were rehydrated in Tween™.

| Character | Mean (SD) Colorado ($n = 7$) | Pacific Northwest ($n = 51$) | $P$ |
|---|---|---|---|
| VAR5 Leaf L (cm) | 3.8714 (1.378) | 4.8314 (1.150) | <.05 |
| VAR6 Leaf W (cm) | 1.4571 (0.469) | 1.8196 (0.444) | <.05 |
| VAR7 Flowers/cluster | 2.8571 (1.069) | 4.4118 (2.376) | NS |
| VAR8 Sepal L (mm) | 7.2857 (1.380) | 8.7549 (1.650) | <.05 |
| VAR9 Sepal W (mm) | 3.2857 (0.488) | 3.8333 (1.109) | NS |
| VAR10 Petal L (mm) | 10.2857 (1.254) | 14.1373 (2.764) | .001 |
| VAR11 Petal W (mm) | 5.8571 (0.900) | 7.8725 (1.466) | .001 |
| VAR12 Stamen L (mm) | 7.4286 (1.512) | 9.4706 (1.669) | <.01 |

## RESULTS AND DISCUSSION

The original descriptions provided by Hooker (1838) and Nelson (1913) differ in language and length, but little in content. In our examination of the plants, we found no qualitative characters, such as color or shape of corollas or shape of leaves, that could be used to distinguish two different species. Likewise, pollen from plants of the two areas was identical. Although Colorado plants tend to be shorter (usually <1 m) than Pacific Northwest plants (1–2 m), and to have smaller leaves and fewer and smaller flowers, these differences may be attributable to phenotypic plasticity in response to the severity of the habitats in which they grow. Elevational range for the Pacific Northwest populations is 1160–2700 m above sea level and weather patterns have an oceanic influence, while for the Colorado populations, the elevational range is 3000–3500 m above sea level and the climate is distinctly continental.

Analysis of the quantitative characters indicated that the means of measurements of leaf length and width, sepal length, petal length and width, and stamen length of the Colorado populations (Table 1) were significantly smaller than the means of the same measurements for the Pacific Northwest populations. However, correlations (Table 2) among the characters that have significantly different means (Table 1) reduce the taxonomic value of those

Table 2. Correlation coefficients among variables measured on specimens of *Rhododendron albiflorum* ($n$ = 58). Variables 1–4 were specimen and locality identification codes. VAR5 = leaf length, VAR6 = leaf width, VAR7 = number of flowers per axillary cluster, VAR8 = sepal length, VAR9 = sepal width, VAR10 = petal length, VAR11 = petal width, VAR12 = stamen length.

| | VAR5 | VAR6 | VAR7 | VAR8 | VAR9 | VAR10 | VAR11 | VAR12 |
|---|---|---|---|---|---|---|---|---|
| VAR5 | 1.0000 | .8284** | .2225 | .2414 | .1053 | .0618 | .0831 | .1632 |
| VAR6 | | 1.0000 | .2721* | .2817* | .1628 | .1084 | .0748 | .2404 |
| VAR7 | | | 1.0000 | .1220 | −.1033 | .0920 | −.3019* | .0862 |
| VAR8 | | | | 1.0000 | .3881** | .5345** | .4620** | .4026* |
| VAR9 | | | | | 1.0000 | .1874 | .2544 | .2075 |
| VAR10 | | | | | | 1.0000 | .6019** | .6156* |
| VAR11 | | | | | | | 1.0000 | .4794* |
| VAR12 | | | | | | | | 1.0000 |

* Significant at the .05 level.
** Significant at the .01 level.

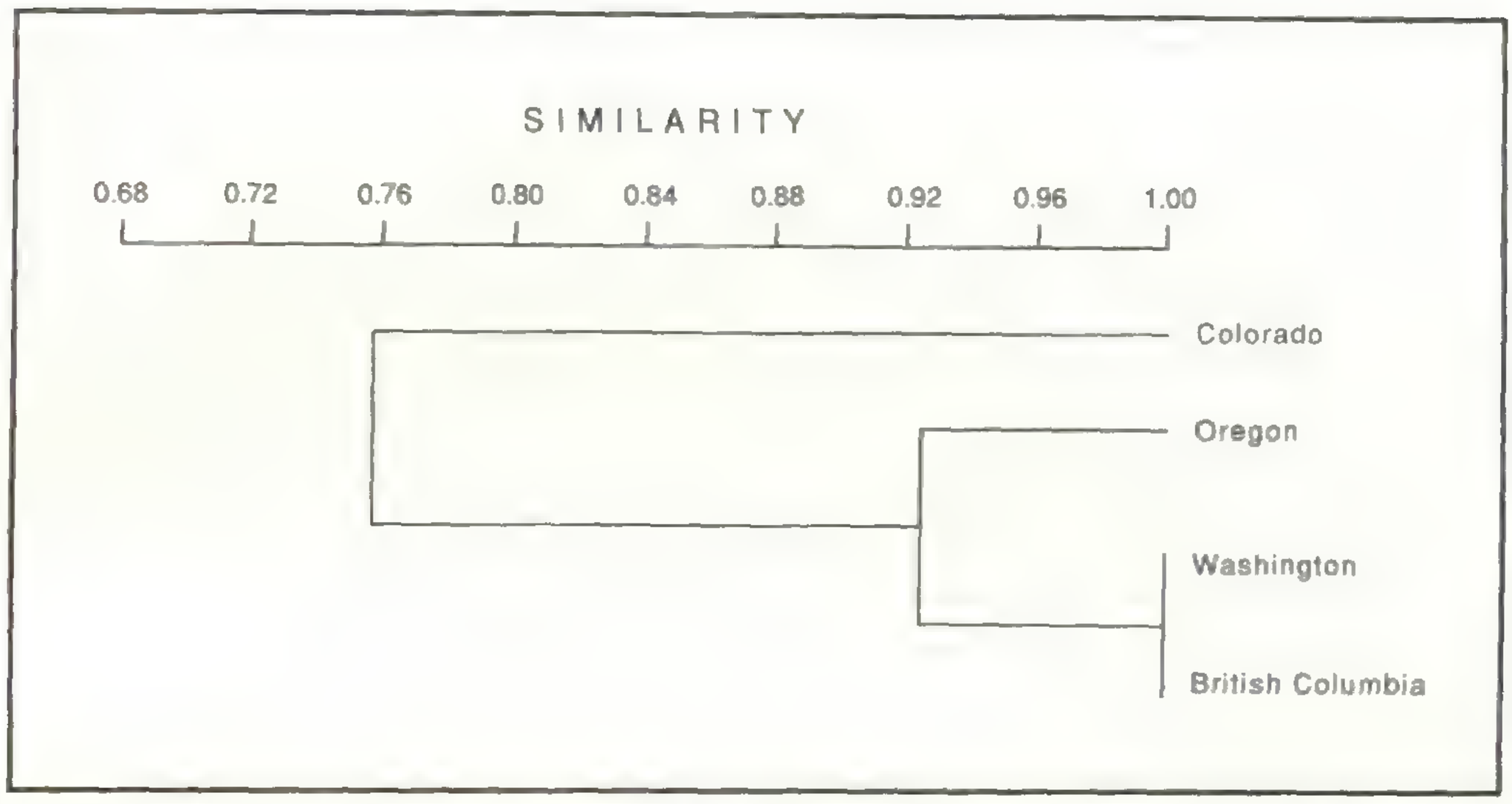


Figure 3. Dendrogram produced by cluster analysis calculated by the unweighted pair group method (Swofford and Selander, 1981) based on unbiased genetic identity (Nei, 1978).

differences. For example, it is reasonable for a shorter petal also to be narrower (VAR10 is correlated at the .01 level with VAR11) or for shorter leaves also to be narrower (the correlation between VAR5 and VAR6 is significant at the .01 level). Even though a discriminant function analysis of the Colorado populations versus the Pacific Northwest populations indicated that petal length and width, and stamen length, accounted for most of the distinction between the groups, the ranges of measurements of these characters for the Colorado populations are either completely within or significantly overlapping with those for the Pacific Northwest populations (Figure 2). Finally, a cluster analysis (not illustrated) performed on all 58 specimens failed to group the 7 Colorado specimens; rather, these populations were scattered among those from Montana, Alberta and Washington. Thus, we conclude that the morphological evidence does not support the recognition of the Colorado plants as a species distinct from that of the Pacific Northwest.

Results from isozymic analysis showed the Colorado populations to be distinct but failed to provide compelling evidence for recognizing these plants at the specific level. As summarized in Table 3 and Figure 3, genetic identity values among the Pacific Northwest populations were consistently above .90 while those between the Colorado and Pacific Northwest populations ranged from .729 to .722. Given that the average genetic identity (Nei,

Table 3. Matrix of similarity and distance coefficients (Nei, 1978) based on data from electrophoretic analysis of 10 enzyme systems. Population acronyms are explained in Materials and Methods. Above diagonal: unbiased genetic distance; below diagonal: unbiased genetic identity.

| Population | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| 1 TIL (Colorado) | — | .273 | .258 | .316 |
| 2 BLR (Oregon) | .761 | — | .118 | .090 |
| 3 ONP (Washington) | .772 | .913 | — | .000 |
| 4 GMR (British Columbia) | .729 | .939 | 1.000 | — |

1978) among congeneric angiosperm species is .67 (Crawford, 1983), our results might be used to suggest that the Colorado populations should be elevated to specific status. However, it is probable that the Colorado populations represent glacial relics (Davis, 1983) that have been isolated for sufficient time to diverge at the isozyme level, but there has been no corresponding morphological divergence except in size.

Thus, the combined data suggest that the most reasonable taxonomic treatment of the two sets of populations is the recognition of two varieties of a single species. The Pacific Northwest plants are referred to *R. albiflorum* Hook var. *albiflorum.*

**Rhododendron albiflorum** Hook. var. **warrenii** (A. Nelson) M. A. Lane, *comb. & stat. nov.*

*Azaleastrum warrenii* A. Nelson. TYPE: Colorado, Jackson Co., lower slope of Mt. Zirkel, 9275 ft., 14 Jul 1911, *E. R. Warren 16* [HOLOTYPE: RM!].

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# SNOW ALGAE IN NORTHERN NEW ENGLAND

BRIAN DUVAL

Algae from the genus *Chloromonas* are known to live in snow in alpine and arctic terrain (Kol, 1968). These cryophilic organisms can be seen as green patches near the surface of snow, typically under the limiting sunlight of a coniferous canopy. Forest litter from spruce and fir may provide nutrients essential for algal growth (Hoham, 1976). Its proliferation is generally sporadic in what often appears to be uniform snowbank habitat. Reports of snow algae in the northeastern United States have all been from the Adirondack Mountains of New York state (Hoham et al., 1989). In May 1992, green snow algae were collected from several peaks in northern New England; this is the first report of snow algae from New England.

Warm spring days and snow meltwater trigger germination and migration of algal cells towards the snowbank surface. In the early morning and evening hours, light conditions are best suited to observe the algae (Hoham, 1975). In May 1992, green and orange snow algal populations were found on Mt. Mansfield and Jay Peak in Vermont, Mt. Washington in New Hampshire, and Mt. Katahdin in Maine. Collections were separately contained in Whirl-pak™ bags packed in snow and transported to the laboratory in a cooler. Parameters such as snowbank depth, elevation and solar exposure were recorded. Light microscopy showed these cells to be *Chloromonas brevispina* Fritsch, or a mix of *C. brevispina* and spindle-shaped cells formally known as *Scotiella cryophila* (Fritsch). The latter are now believed to be asexual spores in the life cycle of a *Chloromonas* that may belong to the species complex of *Chloromonas polyptera* Fritsch (Hoham, 1983, 1992).

In March 1992, algal cells collected from snow on Mt. Greylock, Massachusetts were clearly not members of cryophilic snow algae. However, a complex community of microorganisms including cyanobacteria, fungi, rotifers, ciliates and other protists have been noted on Mt. Greylock. From Mt. Washington, ciliates engorged with green snow algal cells were an interesting component of the snowbank ecosystem.

Fungi belonging to the genera *Chionaster* and *Selenotila* were present in certain snow samples. Cohabitation of snow by cryophilic algae and the fungus *Phacidium* may occur via adherence

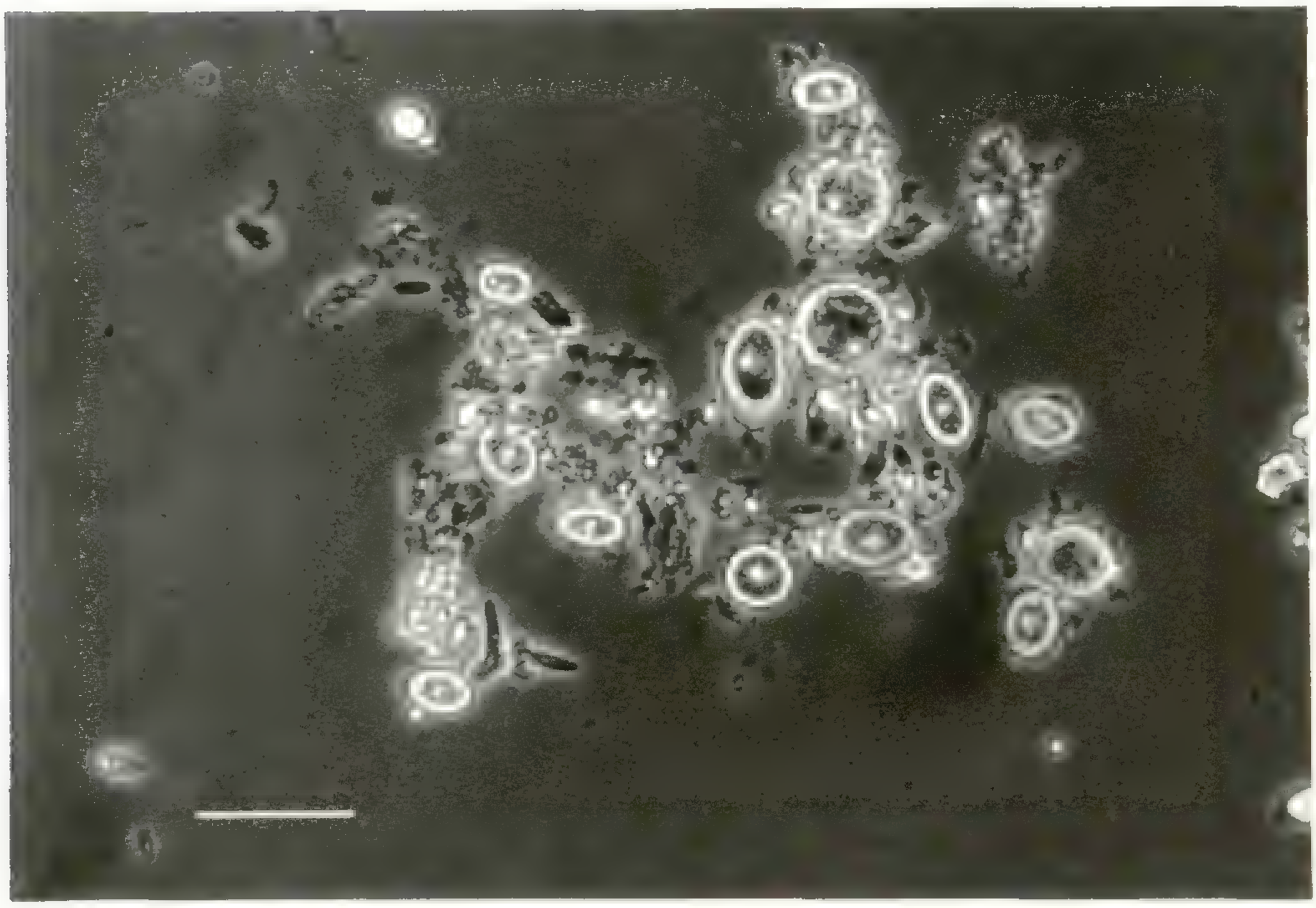

Figure 1. Phase-contrast photomicrograph of orange snow algae, unidentified species, av. 15 × 25 μm (scale bar = 40 μm). Collected from snow (Killington, VT, May 1992).

of algal cells to the web-like filaments of the fungus (Hoham et al., 1989). Snow collected in the Sierra Nevada and Cascade Ranges of California demonstrated this close spatial association (Duval, unpubl.); however, no such relationship was noted in New England snow.

Algal cells with orange carotenoids were found on man-made snow at four New England ski slopes. Secondary pigments serve to protect individual cells from visible and ultra-violet light (Hardy and Curl, 1972). Orange algal populations were found in faint suncups (small depressions in the snow) at the edge of ski trails in relatively open to partially shaded exposures. This organism is probably a new species not reported previously from snow (Figure 1).

Absorption spectra of solvent-extracted pigments from the orange New England snow algae were analyzed. Preliminary analysis of the pigments contained in the cells show absorption only at the wavelengths of 440, 460, and 640 nm; those absorption peaks are typical of *Chloromonas* cells collected in the western United States by the author. Red-pigmented cells of the genus *Chlamydomonas* from western snow have an entirely different spectral

profile. Peak light absorption near the 470 nm wavelength region indicates that carotenoids and xanthophylls are most predominant in the red cells. Thus absorption properties of these orange algal cells from New England appear similar to typical *Chloromonas* (green) rather than *Chlamydomonas* (red) snow algae. Spectrophotometric analysis suggested an ability of certain cryophilic algae to modify their photosynthetic pigments in response to solar exposure (Iturriaga and Sullivan, 1989). However, other studies suggest that nitrogen depletion in snow causes a shift towards secondary carotenoids that protect cells from ultraviolet irradiation (Czygan, 1970; Bidigare et al., 1992).

All snow algal samples are presently being examined and cultured in the laboratory of R. Hoham at Colgate University. This note is a partial report on the distribution of snow algae in New England.

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# A TAXONOMIC STUDY OF *ARISTIDA STRICTA* AND *A. BEYRICHIANA*

ROBERT K. PEET

## ABSTRACT

Grasses traditionally assigned to *Aristida stricta* Michx. include two morphologically and geographically separate species. The name *Aristida stricta* Michx. corresponds to a taxon confined to North Carolina and the northern tier of counties in South Carolina. A second species, *Aristida beyrichiana* Trin. & Rupr., occurs from southern South Carolina south throughout Florida and west to Mississippi.

Key Words: Taxonomy, *Aristida beyrichiana, Aristida stricta,* Poaceae, coastal plain, North America, southeastern U.S.

## INTRODUCTION

The name *Aristida stricta* Michaux has long been applied to those southeastern plants colloquially known as "wiregrass" which dominate the understories of most frequently-burned *Pinus palustris* Mill. and *P. elliottii* Engelm. woodlands and savannas from central North Carolina south to southern Florida and west to eastern Mississippi. No intraspecific variation has previously been described for this taxon. However, the range of *A. stricta, s.l.* has a conspicuous gap in central South Carolina. Further, differences in sheath and blade indument allow plants from north of the gap to be readily distinguished from those south of the gap. In this paper I examine the morphological characteristics, distribution, and taxonomic status of these two types of *Aristida stricta, s.l.* For reasons explained below in the section on taxonomy, I refer to the northern plants as *A. stricta* Michaux and to the southern plants as *A. beyrichiana* Trinius & Ruprecht.

## MORPHOLOGICAL DIFFERENCES

The two variants of *Aristida stricta, s.l.* can be readily and unambiguously differentiated by examination of leaf indument. On plants of the southern *A. beyrichiana,* a densely woolly or villous bearding or tuft of indument is present at the base of the leaf blade (Figure 1). These prominent hairs vary from being distributed on the upper surface of the blade and at the corners of the collar to also (and much more commonly) surrounding the blade, collar, and uppermost portion of the sheath. With age the

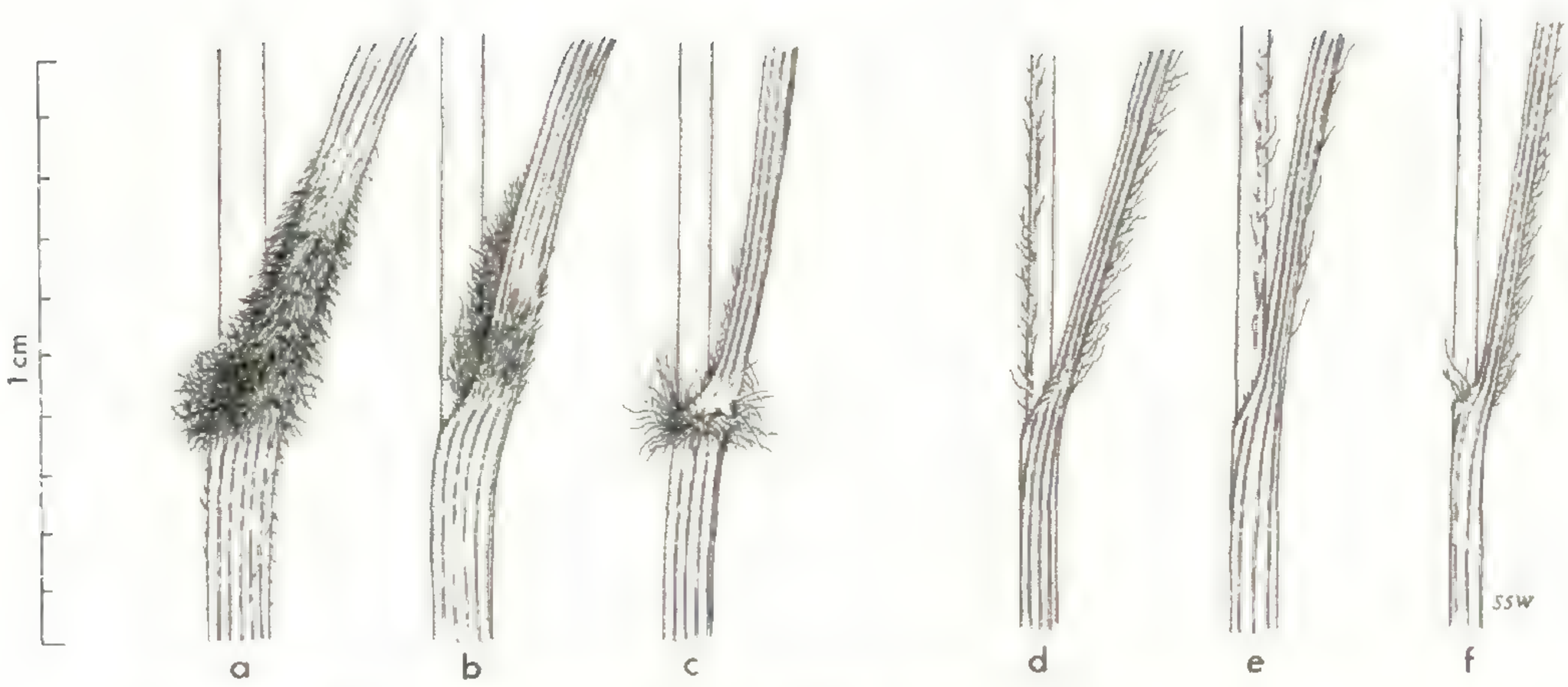


Figure 1. Characteristic blade and sheath pubescence of (**a–c**) *Aristida beyrichiana* Trinius & Ruprecht and (**d–f**) *Aristida stricta* Michaux. In each case the first (**a** and **d**) of the three figures is the most typical and the other two illustrate some of the range of variation.

hairs can be partially deciduous, but they are always evident on the younger foliage and, together with the involute leaves, allow *A. beyrichiana* to be distinguished in vegetative condition from all other southeastern North American grasses. Individual plants can differ substantially in amount of indument, but at a minimum, plants of *A. beyrichiana* have numerous hairs protruding from about the throat and corners of the collar. In contrast, the northern *A. stricta* lacks this localized bearding or tuft. At most, there may be a few prominent hairs at the corners of the collars of the most hairy plants, and on most plants there are no hairs except for those on the back of the blade as described below.

The northern *Aristida stricta, s.s.* is readily distinguished in vegetative condition from all other native grasses by the presence of a line of villous indument (hairs .6–1.5 mm long) adjacent to and on each side of the midrib along the length of the back of the involute blade (Figure 1). The hairs can be deciduous with age, but are always present on the younger foliage. The foliage of the southern *A. beyrichiana* usually lacks indument on the backs of the leaves except for the characteristic woolly to villous tufts or bearding at the bases of the blades. The one exception is that seven percent of the Florida specimens examined (17 of 251) had foliar indument along the midrib; the trait was not observed in collections of *A. beyrichiana* from any other state. In those few Florida plants where the lines of villous indument were present on the foliage, the diagnostic wooly tuft or bearding at the base of the blade was particularly conspicuous.

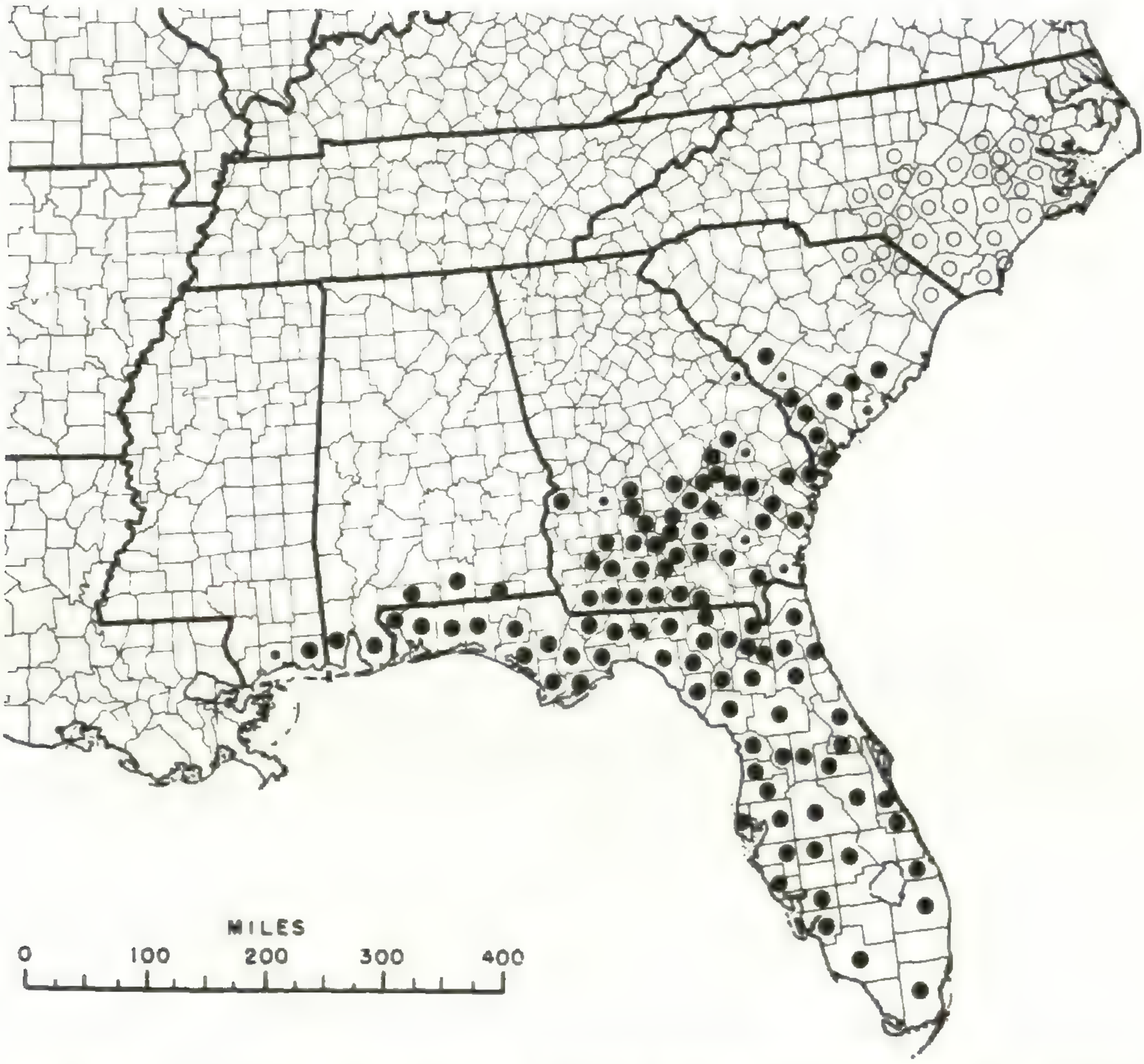


Figure 2. County distribution of *Aristida stricta* Michaux (○) and *Aristida beyrichiana* Trinius & Ruprecht (●). Unverified reports are indicated by (•).

Other differences between the taxa can be observed, but they are generally minor and often statistical. For example, the average ligule length is less for *Aristida stricta,* as is culm width, and, on average, the glumes are more unequal in *A. beyrichiana.*

## DISTRIBUTION

I examined all specimens labeled as *Aristida stricta* Michx. held by the following herbaria: CLEMS, DUKE, FLA, FLAS, GA, GH, L, MO, NCSC, NCU, NY, P, UAL, US, USCH, VDB and Southern Mississippi. County range maps were drawn using data on the 564 specimens examined that were assignable to county of origin (Figure 2).

Nine counties within the range of *Aristida beyrichiana* for which I could not locate specimens to authenticate reliable reports are indicated on the map by small dots: Sumter County, Georgia

(Jones and Coile, 1988); Camden, Candler, Pierce and Richmond Counties, Georgia (Bozeman, 1971); Harrison County, Mississippi (Eleuterius and Jones, 1969); and Barnwell and Charleston Counties, South Carolina (Radford et al., 1968). A record from Oglethorpe County, Georgia, in Jones and Coile (1988) is based on an incorrectly identified collection (GA No. 133102). Blomquist (1948) indicated a record of *Aristida stricta* for Pasquotank County, North Carolina. Despite my examination of all of the herbaria Blomquist reported consulting, I have found no specimen to support that record. Because Pasquotank County is located well north of the known range of the species, I have not indicated this record on the map, although appropriate habitat does occur within the county.

The ranges of *Aristida stricta* and *A. beyrichiana* are not only distinct, but clearly separated (Figure 2). Neither species has been found in central South Carolina. The one near intrusion of the range of *A. beyrichiana* into the central part of South Carolina is in Berkeley County, where the species is known only from a single locality from which it appears to have been extirpated. Examinations of likely habitats in central South Carolina, including the sandhills around Columbia and the pine flatwoods of the Francis Marion National Forest nearer the coast failed to locate either species.

*Aristida stricta* Michx. is almost a North Carolina endemic, occurring only in North Carolina and the northern most counties of South Carolina. In this area the species is particularly common on coarse sands dominated by *Pinus palustris,* both in the fall-line sandhills and on the flatlands of the outer coastal plain (Frost et al., 1986; Peet and Allard, 1993). Examination of the distribution of the southern wiregrass, *Aristida beyrichiana,* shows that in the northeastern portion of its range it is largely concentrated in those counties that contain the dune systems characteristic of the northeast sides of major rivers (e.g., the Savannah and Altamaha Rivers). In the western portion of its range, the species is confined to the southernmost tier of counties along the Gulf of Mexico.

The ranges of the two species that make up the *Aristida stricta, s.l.* complex are not atypical of the ranges of other species of the southeastern pinelands. Indeed, so many species have similar ranges that it seems likely that there were two main centers of persistence of the pineland flora during the last full glacial: one

near but perhaps east of what is now southeastern North Carolina, and another along the Gulf coast. Species with ranges similar to that of *A. stricta, s.s.* and essentially endemic to the pinelands of North Carolina and adjacent South Carolina include *Dionaea muscipula* Ell., *Kalmia cuneata* Michx., *Lysimachia asperulaefolia* Poir., *Lysimachia loomisii* Torr., *Pyxidanthera brevifolia* Wells, *Solidago pulchra* Small, *Solidago verna* M. A. Curtis, *Sporobolus, sp. nov.* (*aff. teretifolius* Harper; a dominant of moist savannas), *Tofieldia glabra* Nutt., *Vaccinium crassifolium* Andr. and *Zenobia pulverulenta* (Bart. *ex* Willd.) Pollard. In addition, *Calamovilfa brevipilis* (Torr.) Scrib., *Gentiana autumnalis* L. and *Pyxidanthera barbulata* Michx. have similar ranges, but also have disjunct populations in the pine barrens of New Jersey. Among species that, like *Aristida beyrichiana,* have ranges that extend from the Gulf coast north to southernmost South Carolina are *Asclepias cinerea* Walt., *Astragalus villosus* Michx., *Baptisia lanceolata* (Walt.) Ell., *Gaylussacia tomentosa* (Gray) Small, *Gaylussacia mosieri* Small, *Helianthus radula* (Pursh) Torr. & Gray, *Kalmia hirsuta* Walt., *Liatris gracilis* Pursh, *Pinus elliottii* Engelm., *Sabatia bartramii* Wilbur, *Sabatia brevifolia* Raf., *Serenoa repens* (Bartr.) Small, *Sorghastrum secundum* (Ell.) Nash and *Vaccinium myrsinites* Lam.

## TAXONOMY

The two taxa included in *Aristida stricta, s.l.* are quite similar and are obviously closely related. Because they are readily and consistently distinguishable morphologically and are geographically separated as well, I have chosen to treat them as separate species.

Michaux's original description of *Aristida stricta* [Fl. Bor. Amer. 1: 41. 1803]. reads "A. culmis foliisque stricte erectis: foliis pubescentibus: racemo in spicam longam, angustam, non ita confertam coarctato: aristis gluma longioribus. Obs. Variat foliis planiusculis et convoluto-filiformibus. Hab. in Carolina inferiore." The reference to "foliis pubescentibus" is certainly suggestive of the northern species with its conspicuous pubescence along the back sides of the leaf blades, but the description alone is insufficient to determine definitively which taxon Michaux collected and described.

Although Michaux (1803) reported that his type collection of

*Aristida stricta* was from "Carolina inferiore," Michaux's annotation on the label reads only "Hab. in Carolina." L. M. C. Richard is widely believed to have anonymously written Michaux's text, some of it after Michaux's death (Hitchcock, 1908; Stafleu and Cowan, 1981; Uttal, 1984) and many of the habitat locations in the text differ from those on the specimen labels. The basis for designating South Carolina rather than simply Carolina as the collection locality in Michaux (1803) remains unclear.

Michaux described in his journal (Sargent, 1889) numerous trips through pine barrens between Charleston, South Carolina, and Charlotte, North Carolina, and along the coast past Wilmington, North Carolina, both areas which today are dominated by the northern *Aristida stricta.* Michaux is also known to have collected widely in the regions where the southern *A. beyrichiana* dominates. In short, it does not appear possible to determine from published records where in the Carolinas Michaux collected his *Aristida stricta.*

The type of *Aristida stricta* is in the Michaux Herbarium at Paris. The Michaux Herbarium contains two specimens labeled *Aristida stricta.* However, only one has the annotation "Hab. in Carolina." As Michaux (1803) reported the type as being from "Carolina inferiore," this specimen appears to be the type, a conclusion also reached by Hitchcock (1908) and Henrard (1928). The specimen is a mixed collection. The larger culm bases have had their inflorescences broken off and appear to represent some species other than *A. stricta* or *A. beyrichiana.* These culm bases have ligules 1.5 to 2.0 mm long, significantly longer than the .02 to .2 mm range normally encountered in *Aristida stricta* and *A. beyrichiana,* and longer than any I observed in the over 650 herbarium specimens I examined. In addition, they differ from both species in that they are almost entirely devoid of indument. However, there are two separate young, sterile culms (with ligules .1 mm long) and several separate but older leaf blades that have the distinctive villous indument ("foliis pubescentibus," Michaux, 1803) along the sides of the midrib that characterize the northern *Aristida stricta.* They also lack the tuft of hairs at the throat and corners of the collar typical of the southern species. Because *Aristida stricta* and *A. beyrichiana* have similar flowers and inflorescences, I cannot be absolutely certain which species the fertile portion of the type collection represents. The combined collection was interpreted as the type by Hitchcock (1908) and

Henrard (1928), but the pubescent foliage is the only portion unambiguously assignable to a single species. Thus, the pubescent young culms and pubescent older foliage on this specimen should probably be taken as the type of *A. stricta.*

The other specimen in the Michaux Herbarium labeled *Aristida stricta* is a flat-bladed species, almost certainly *Aristida purpurascens* Poir. The original Michaux description of *Aristida stricta* has the confusing line "Variat foliis planiusculis et convoluto-filiformibus" which suggests that the description mixes the leaf blade characteristics of the two species represented by the two Michaux Herbarium specimens labeled *Aristida stricta.* The "convoluto-filiformibus" foliage trait (unlike "planiusculis" foliage) is characteristic of a single species in the region, and "foliis pubescentibus" is consistent with that species, which provides further reason to apply the name *A. stricta* to the species with involute, pubescent leaves.

There is a third Michaux collection labeled *Aristida stricta* in the General Herbarium at Paris which has been referred to by Henrard (1928) as an isotype from the Richard Herbarium. This collection is more complete than the collection in the Michaux Herbarium, has conspicuous villous indument along the length of the midvein, and is unambiguously the northern form. My suspicion is that this specimen was also examined when Richard or Michaux wrote the original description of *Aristida stricta* for Michaux's 1803 text, simply because it is the only specimen with all the leaves conspicuously hairy.

In 1849, Trinius and Ruprecht described a new species, *Aristida beyrichiana* Trin. & Rupr. (Mém. Acad. St. Pétersb. VI. Sci. Nat. 7(2): 104. 1849), which they recognized as distinct from *Aristida stricta.* However, their description of *A. beyrichiana* has not been adequate for others to make a distinction; as a consequence, all subsequent authors have viewed *A. beyrichiana* as a synonym of *A. stricta.* Further, because the description only addresses the inflorescence, it is not possible to assign the description to either of the taxa recognized in the present paper. In his monograph of North America *Aristida,* Hitchcock (1924) stated that he thought the type of *Aristida beyrichiana* to be an immature *A. stricta,* although he admitted uncertainty. He had examined a fragment of the type in US (No. 81011), but apparently had not seen the holotype in LE. Henrard (1926) reported in his monograph of *Aristida* that "This is a plant with awns not yet fully developed,

but agrees for the rest with *A. stricta* Michx., having the striking villous tuft at the throat of the sheaths," a sure indication that he was examining the southern species.

I have examined the fragment at US (No. 81011), and a Beyrich collection at L (No. 908.83-1016) that Henrard (1926) referred to as an isotype. I found them both consistent with Henrard's description. The villous tufts are present on the US fragment, indicating that it is *Aristida beyrichiana,* although the tufts are smaller than average, and the blades are both a little wider and not quite as closely involute as is normally encountered. However, the L specimen is unambiguously the southern species with villous bearding at the leaf base extending onto the collar, and with typical leaf dimensions. The spikelets on both specimens are, as Hitchcock (1924) and Henrard (1926) reported, not fully mature.

The type locality for *Aristida beyrichiana* remains uncertain, but is probably Georgia. Trinius and Ruprecht reported that the Beyrich specimen they described originated "In pinetis Georgiae et in territorio Arkansas." However, this description may simply represent the general area in which Beyrich collected; he is also known to have collected in both North and South Carolina (Sayre, 1975). Henrard (1926) reported that the label on the type reads simply "Georgia in pinetis (Beyrich)," but this observation almost certainly derives from the label on the putative isotype at L, which it matches exactly.

Virtually all modern descriptions of *Aristida stricta* match the species I call *A. beyrichiana.* For example, Hitchcock (1924, 1935), Henrard (1932), Godfrey and Wooten (1979) and Allred (1986) all make reference to the distinctive villous tuft at the base of the leaf blades as characteristic of the species. Interestingly, Henrard (1932) reported the range of *Aristida stricta* as South Carolina to Florida and Mississippi, exactly the range of *A. beyrichiana.* There are no specimens of *Aristida stricta, s.s.* in the Leiden Herbarium where Henrard worked that are old enough to have been in the collection when he was active. Except for the type in Paris, there is no evidence that Henrard ever examined specimens of the true *A. stricta.*

Trinius and Ruprecht (1849) listed *Aristida lanuginosa* Clarion (Trinius and Ruprecht, Mem. Acad. St. Petersb. VI. Sci. Nat. 4(2): 46. 1838) as a synonym of *A. stricta.* The original 1838 reference contains the name only, and a formal description first appeared in Trinius and Ruprecht (1849) where reference was

made to a specimen in the Mertens Herbarium (LE) with the name *A. lanuginosa* Bosc. (thus the appropriate citation is *A. lanuginosa* Bosc *ex* Trin. & Rupr.).

Hitchcock (1924) reported that there is a Bosc specimen from South Carolina in the Padua Herbarium labeled *Aristida lanuginosa,* which is really *A. lanosa* Muhl. ex Ell. In 1924, Hitchcock declared *A. lanuginosa* to be a synonym of *A. lanosa,* but there is no evidence that he ever examined the type specimen. Like Hitchcock, Henrard (1927) stated that Bosc's plant is unambiguously the previously described *Aristida lanosa,* a conclusion that probably derives from observation of a Bosc collection in P labeled *A. lanuginosa* (probably an isotype), but which is certainly *A. lanosa.* Thus, it is extremely unlikely that the name *A. lanuginosa* refers to the southern species of *Aristida stricta, s.l.,* but if it did it would be the oldest name other than *A. stricta* to be applied to the southern taxon. However, there has been described an *A. lanuginosa* Burch. (Burchell, 1824), which is a later synonym of *A. vestita* Thunb. As the 1824 name is validly published (*see* Henrard, 1927: 287), *A. lanuginosa* Bosc *ex* Trin. & Rupr. is a later homonym and could not be applied to the *A. beyrichiana* material, even if the type proved to be this taxon.

## KEY AND SPECIES CHARACTERIZATION

Base of blade, collar, and upper sheath lacking a conspicuous tuft or bearding of woolly to villous indument; current-year leaves with villous indument along the sides of the midrib on the lower surface for most of the length of the blade ..... **1.** *Aristida stricta*

Base of blade and collar (and often upper sheath) with conspicuous tuft or bearding of woolly to villous indument, always present on current-year foliage but sometimes deciduous on older foliage; leaves usually glabrous above the basal 2 cm of the blade ..... **2.** *Aristida beyrichiana*

1. **Aristida stricta** Michaux, Fl. Bor. Amer. 1: 41. 1803. *Chaetaria stricta* (Michx.) Beauv. Ess. Agrost. 30, 152, 158. 1812; not *Aristida stricta* Muhlenberg, Descriptio uberior Graminum. 174. 1817. TYPE: Carolina (HOLOTYPE: P, Michaux Herbarium!; fragment US No. 81246, but insufficient material for determination; ISOTYPE: P, General Herbarium!).

Plants perennial; culms cespitose, erect, 60–120 cm; sheaths glabrous, occasionally with a few prominent hairs at the corners of the collars but typically absent with the collars glabrous; blades closely involute, .3–1.0 mm thick when rolled, to 50 cm long, mostly emerging near base, firm and somewhat flexuous, upper surfaces scabrous with some hairs up to 1.0 mm long, hairs on the upper surface hidden within the rolled leaf or with a few emerging along the lower 5 cm, villous on the lower surface along sides of midrib with hairs .6–1.5 mm (i.e., often over twice the width of the leaf) all along the length of the blade or at least along the lower 20 cm, hairs sometimes deciduous with maturity but always present on young foliage; ligules minute to nearly absent, membrane to .1 mm, lacerate or composed of flat hairs to .1 mm; panicles long and slender, 20–35 cm long, branches appressed, floriferous from the base; glumes somewhat unequal, awns 1.5–2.5 mm, awns usually emerging from bifid tips; first glume 7–10 mm, 1-nerved or with an additional nerve on one side, scaberulous on the keel but otherwise glabrous; second glume 9–12 mm, 1-nerved, glabrous, if scabrous on the keel then only near the summit; lemma 6–9 mm, shorter than the second glume, glabrous except for the densely short-pilose callus, callus .4–.6 mm; awns of lemma 3, somewhat unequal, sharply divergent with maturation, central awn 10–15 (22) mm, lateral awns usually 1–2 mm shorter.

RANGE. Coastal plain of the Carolinas from the Pamlico River on the north to the northern tier of counties in South Carolina.

2. **Aristida beyrichiana** Trinius & Ruprecht, Mém. Acad. St. Pétersb. VI. Sci. Nat. 7(2): 104. 1849. TYPE: Georgia? ("In pinetas Georgiae et in territorio Arkansas.") (HOLOTYPE: LE, Trinius Herbarium, not seen, *fide* Henrard, 1926; fragment US! No. 81011; ISOTYPE: L!, No. 908.83-1016, *see* Henrard, 1926).

Plants perennial; culms cespitose, erect, 40–120 cm; sheaths glabrous except at the summit, copiously to somewhat villous on the upper .5 cm, especially about throat and collar, always with prominent protruding hairs at the corners of the collar; blades closely involute, .3–1.0 mm thick when rolled, to 20–40 cm long, mostly emerging near base, firm and somewhat flexuous, upper surfaces scabrous with few to many hairs protruding near base

up to 1.0 mm, lower surface somewhat to copiously villous to woolly at the base, but usually glabrous beyond the lowest 1–3 cm (at maturity, villous indument is sometimes deciduous, but young culms always possess this woolly tuft), those few plants with indument somewhat persistent along sides of midrib on underside along lower 20–30 cm of blade as in *A. stricta* are always copiously hairy at the bases of blades and on the sheaths, and are woolly to villous around the collars; ligule membrane .05–.3 mm, behind which are often conspicuous hairs; panicles long and slender, 15–30 cm long, branches appressed, floriferous from the base; glumes subequal, with awns 1.5–2.5 mm from bifid tip; first glume 7–10 mm, 1-nerved or with an additional nerve on one side, glabrous on the back but keel scaberulous; second glume 8.5–11 mm, 1-nerved, glabrous, scabrous only on keel or not at all; lemmas 6–8 mm, shorter than the second glume, glabrous except for densely short-pilose callus, callus .4–.6 mm; awns of lemma 3, somewhat unequal, sharply divergent with maturation, central awn 7–14 mm, lateral awns usually 1–2 mm shorter.

RANGE. Southeastern coastal plain from southern South Carolina south to Dade County, Florida, and west along the coastal counties to at least Jackson County, Mississippi.

## ACKNOWLEDGMENTS

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# A REVISION OF THE *CHAMAESYCE DELTOIDEA* (EUPHORBIACEAE) COMPLEX OF SOUTHERN FLORIDA

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## ABSTRACT

Morphological investigation of the *Chamaesyce deltoidea* complex demonstrates a lack of sharp boundaries between the taxa. In combination with distributional data, the observed patterns of morphological variation suggest that the complex is best treated as a single polymorphic species. New combinations are proposed for *Chamaesyce pinetorum* and *C. adhaerens* to provide a consistent treatment for the morphological groups within the complex. The current conservation status of each morphological group is reviewed.

Key Words: *Chamaesyce deltoidea,* subspecies complex, endangered species, geographical distinction, south Florida

*Chamaesyce deltoidea* (Engelmann) Small represents a complex of four closely related taxa found in the rocky pinelands south of Miami and similar pinelands on the lower Florida Keys (Figure 1). Three of the taxa are currently listed as endangered (Bentzien, 1985; listed under the name *Euphorbia deltoidea*), and a clear understanding of taxonomic limits within the complex is required for proper application of provisions of the Endangered Species Act. However, current treatment of the group (Burch, 1965, 1966) does not satisfactorily account for patterns of variation found within the complex.

*Euphorbia deltoidea* Engelmann ex Chapman was the first member of the complex to be described. It was included in the appendix (p. 647) of Chapman (1883). This species was transferred to the genus *Chamaesyce* by Small (1903, p. 710, 1033). During the following three decades, Small proposed three new species closely related to *C. deltoidea*: *C. pinetorum* (Small, 1905), *S. serpyllum* (Small, 1913, p. 81, 155), and *C. adhaerens* (Small, 1927). Members of the complex are characterized by wiry stems radiating from a woody taproot, thick leaves with shallowly cordate bases, cyathia on short peduncles solitary in leaf axils, and minute or absent gland appendages. These four taxa are endemic to southern Florida. Several West Indian species, particularly *C.*

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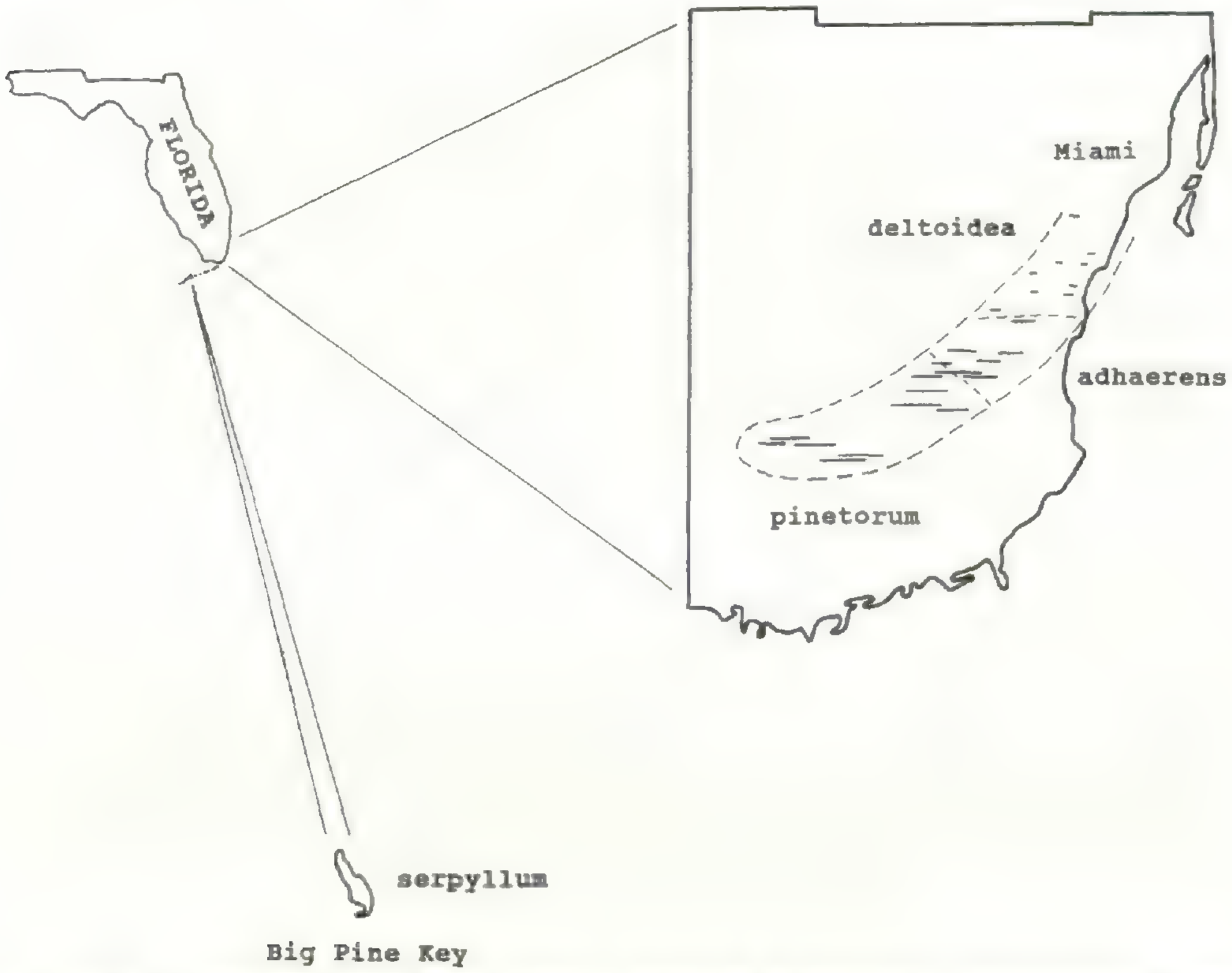


Figure 1. Map of southern Florida showing geographical distribution of the four subspecies in the *Chamaesyce deltoidea* complex, and distribution in trichome lengths for the three mainland subspecies. Each bar represents a separate population; length of bar is proportional to length of stem and leaf trichomes in the population. Only populations with accurately known locations are mapped.

*turpinii* (Boissier) Millspaugh [including *C. puertoricensis* (Urban) Millspaugh] and *C. centunculoides* (H.B.K.) Millspaugh are closely related to the *C. deltoidea* complex, but are easily distinguished by possession of gland appendages equalling or exceeding the gland in width.

In Small's final treatment of the complex (Small, 1933), each member was considered to represent a distinct species. Major characters used to define the species were habit and pubescence. Minor distinctions were also noted in seed and cyathium characters (Table 1). More recently, Burch (1966) grouped the four members of the complex into two species distinguished from each other by habit. *Chamaesyce deltoidea* included all populations having prostrate stems (Small's *C. adhaerens, C. deltoidea* and *C. serpyllum*) while *C. pinetorum* included all plants with erect or ascending stems. This treatment was adopted by Long and Lakela (1971). The most recent study of this complex was that of Remus (1979), and it purported to support Burch's treatment.

Table 1. Characters used by Small (1933) in distinguishing among the taxa of the *Chamaesyce deltoidea* complex.

| Character | *C. adhaerens* | *C. deltoidea* | *C. pinetorum* | *C. serpyllum* |
|---|---|---|---|---|
| Habit | prostrate | prostrate | ascending | prostrate |
| Pubescence | villous-hirsutulose | glabrous | villous-hirsute | puberulent-canescent |
| Leaf shape | as long as wide | as long as wide | ——* | longer than wide |
| Cyathium length | about 1 mm | less than 1 mm | 1 mm | less than 1 mm |
| Seed length | about 1 mm | less than 1 mm | 1 mm | less than 1 mm |

* This character not reported by Small.

However, Remus used the name *Chamaesyce adhaerens* for different plants than Small, and his conclusions actually imply a closer relationship between Small's *C. adhaerens* and *C. pinetorum* than between *C. adhaerens* and *C. deltoidea.*

In this study, a modified key for identification of the taxa is presented and relationships between taxa are discussed. The four taxa of Small are all treated as subspecies of *Chamaesyce deltoidea.* Only the subspecies designations are referred to in the text below.

## MATERIALS AND METHODS

A survey of all extant potential habitat was carried out during the years 1980–81. Materials from throughout the current range of the taxa were collected for analysis during this study. Additional herbarium specimens were borrowed to supplement these collections. A total of 277 specimens was examined.

Several characters were measured on dried specimens. Leaf length was measured along the midvein and leaf width was measured perpendicular to the midvein at the widest point of the leaf on up to five fully-exposed, flat leaves per sheet. Cyathium length and width (measured across the glands) were measured for up to seven cyathia per sheet. When available, cyathia with staminate or pistillate flowers at anthesis were measured, otherwise cyathia with young or mature fruit were measured. Seed length was measured along the long axis of the seed using an optical comparator. Trichome length was measured or, when the trichomes were curved or bent, estimated on stem, leaves and cyathia using an optical

comparator. Trichome density on stems and leaves was scored following the method of Isley (1953) where samples were assigned to density classes on the basis of the ratio between average trichome length and the average distance between trichomes. The youngest fully expanded leaves and the stem sections immediately below them were used for trichome density estimates. Trichome length was most conviently measured near the tip of a stem.

Specimens preserved in Formalin–Acetic Acid–Alcohol or 95% Ethyl Alcohol were available for several populations covering the entire current range of the complex. Cyathium length and width measurements were taken from these specimens to verify and supplement results obtained from dried specimens.

## RESULTS

Bar graphs of seed length (Figure 2) show a large degree of overlap among all four taxa. Seed length in ssp. *serpyllum* averages lower than in the other three subspecies, but the significance of this difference is obscured by the large degree of overlap with other subspecies. In the other characters used by Small, a similar picture is presented. In the few cases where average differences are found between subspecies, such as leaf shape, where ssp. *serpyllum* has narrower leaves in general than other taxa, overlap between taxa is extensive.

Cyathium width proved to be an unsatisfactory character to measure from dried specimens due to variations in the amount of pressure on different cyathia during drying. Measurements taken from liquid-preserved material (Figure 3) showed that variation within populations was always high and often a large fraction of the total variation found within the complex. No consistent differences in cyathium size or shape were found to separate the taxa.

Populations of ssp. *deltoidea,* ssp. *pinetorum* and ssp. *serpyllum* are easily identifiable, each having a distinct set of morphological characteristics. Subspecies *deltoidea* is characterized by prostrate stems, a predominantly short-shoot growth form with internodes shorter than leaf width, stems and leaves glabrous or very sparingly pubescent, and appressed uncinate trichomes. Subspecies *pinetorum* has erect or ascending stems, a predominantly long-shoot growth form with internodes usually 1.5 to 2 × leaf width, and a dense covering of long, straight, spreading hairs. Subspecies

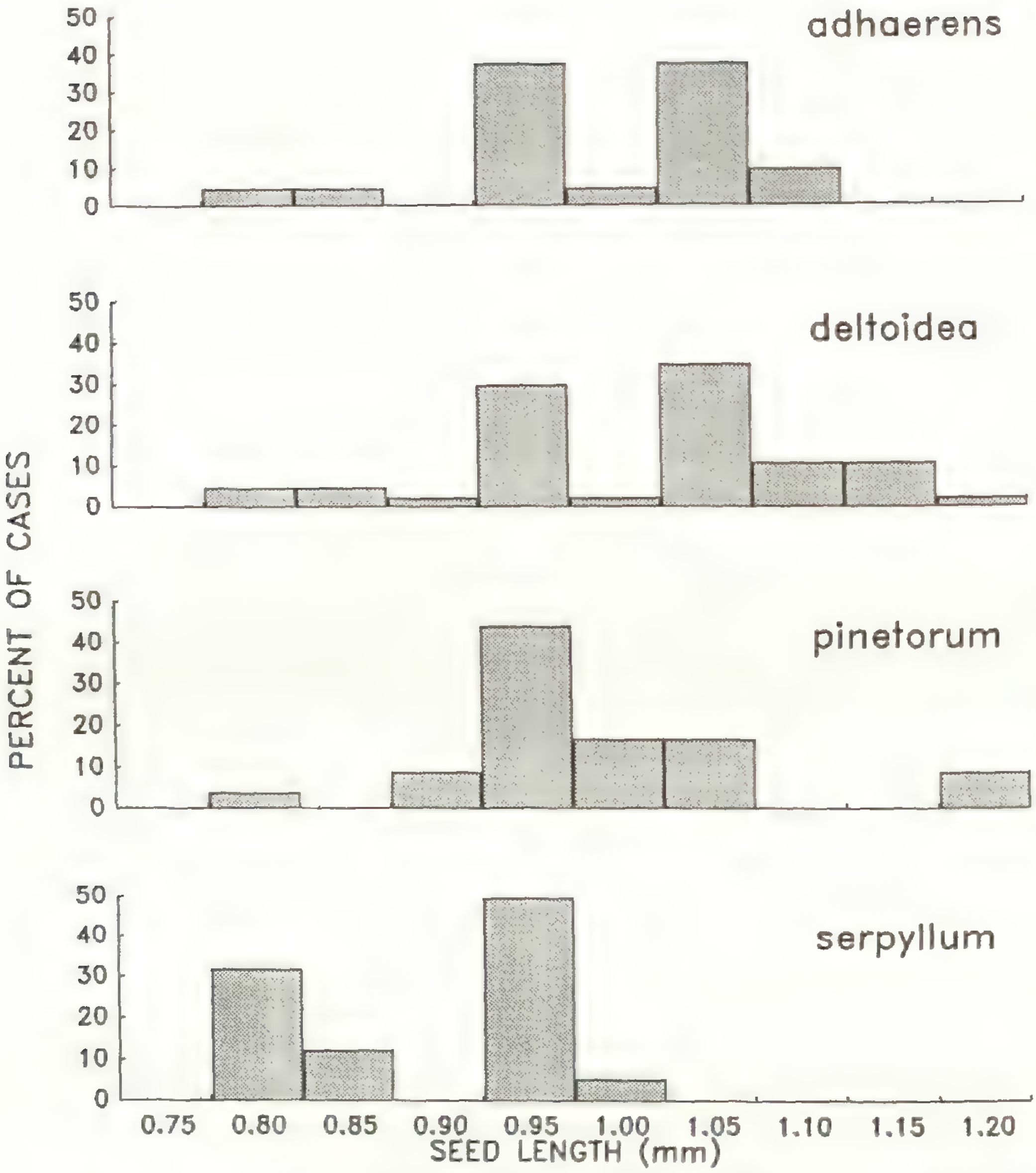


Figure 2. Bar graphs showing distribution of seed lengths in the four subspecies of the *Chamaesyce deltoidea* complex (based on measurements of 25 seeds for each subspecies). Degree of overlap demonstrates that this character cannot be used to distinguish among the taxa.

*serpyllum* is characterized by prostrate stems, a predominantly long-shoot growth form, and a very dense pubescence (which gives the plant a silvery appearance) of appressed, irregularly twisted trichomes.

Subspecies *adhaerens* is here defined in terms of pubescence characters alone. It has appressed uncinate trichomes on leaf surfaces and twisted, ascending to spreading, trichomes on stem surfaces. Trichome length, trichome density and plant habit vary in a clinal fashion across the range of ssp. *adhaerens*. At the

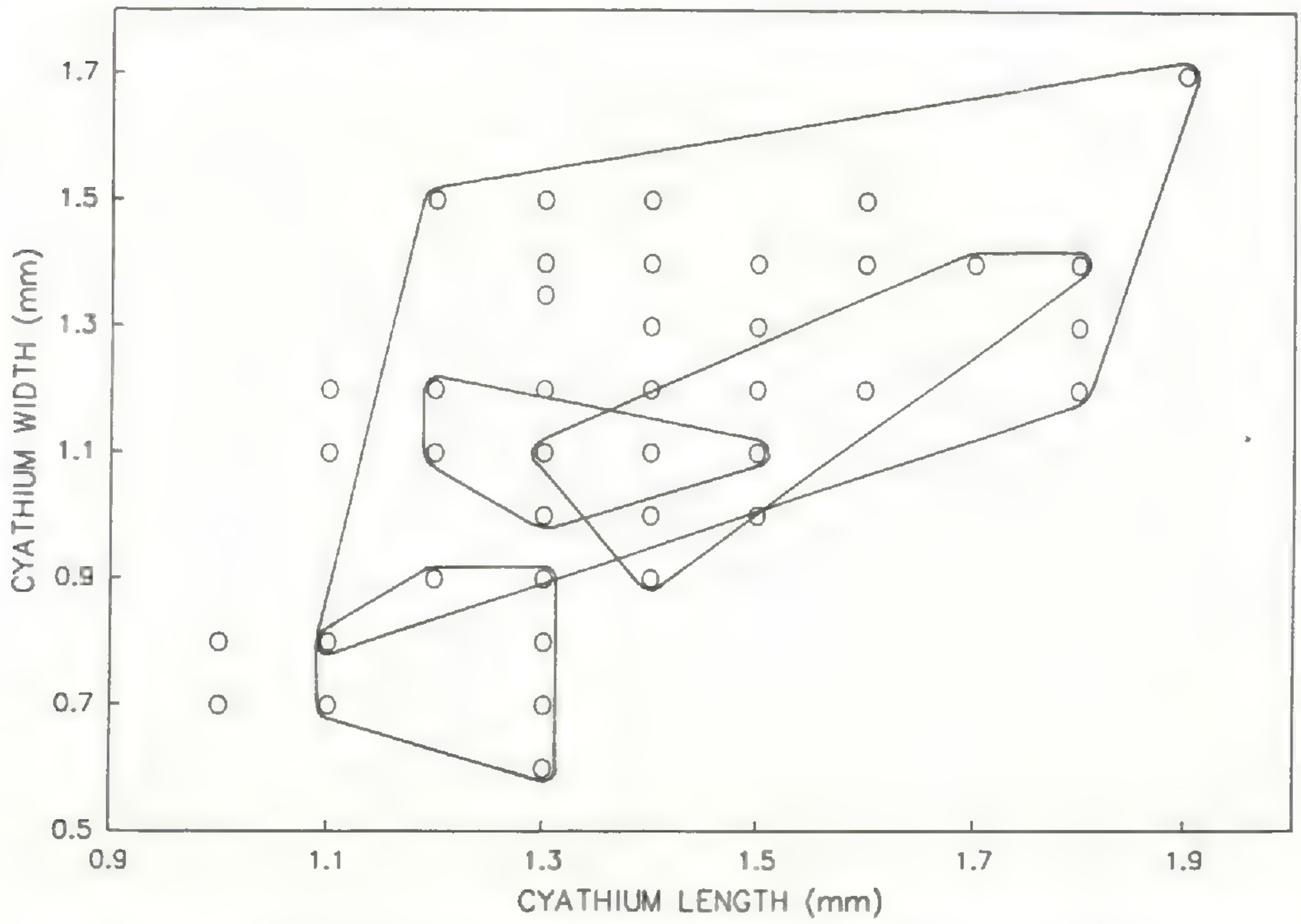


Figure 3. Scatter diagram of length and width measurements taken from liquid-preserved cyathia. Curves enclose measurements from four populations. Variability within single populations is often a large fraction of the total variability observed in the complex.

northern end of its range it approaches ssp. *deltoidea* in appearance, and at the southern end, it grades into ssp. *pinetorum*.

## DISCUSSION

Subspecies *pinetorum* is not isolated from other members of the complex as the current classification (Burch, 1966) implies; it forms an evolutionary unit equivalent to ssp. *deltoidea* or ssp. *serpyllum*. The taxonomic rank of the three groups of populations is hard to define. They are more strongly differentiated than most subspecific taxa, and, if ssp. *adhaerens* were not present, could easily be considered weakly separated species. But, for the reasons given below, I treat them here as members of a single polymorphic species.

The differences between all four members of the complex are vegetative and no differences have been found in their life histories or modes of reproduction. The vegetative characters used to define the differences are found to vary in a clinal fashion in the mainland populations, and these populations seem to inter-

grade along broad zones of contact. Differences between the populations of ssp. *serpyllum* on the Florida Keys and the mainland subspecies are no different in kind than the differences between the extreme forms of the mainland subspecies. Finally, there is no geographical overlap of different morphological types to suggest barriers to interbreeding. One specimen of ssp. *adhaerens* preserved at NY (*Small & Carter 860*) indicates a collection locality (by an arrow drawn on a map of Dade Co.) within the range I have defined for ssp. *pinetorum.* Another specimen of ssp. *deltoidea* at NY (*Small & Wilson 1979*) similarly indicates a collection locality outside of the range shown for ssp. *deltoidea* in Figure 1. No detailed information on the locality of either collection has been located nor has any reference by Small to finding any subspecies growing together. Burch (1965) stated that ssp. *pinetorum* is broadly sympatric with ssp. *adhaerens* and ssp. *deltoidea,* but this assertion is not supported by any specimens I have seen. Since neither the precisely located collections of Burch nor my own field survey produced any examples of two members of the complex growing together, I do not consider these suggestions of range overlap credible.

In addition to the arguments presented above, it is relevant that qualitative differences in pubescence can be found within other species of *Chamaesyce.* In particular, *C. turpinii,* as presently understood, has essentially the same range of pubescence types as do pubescent forms of *C. deltoidea.* In a different group, the current conception of *C. polycarpa* (Bentham) Millspaugh encompasses both glabrous and pubescent plants.

Populations of ssp. *adhaerens* bridge the morphological gaps between the other three taxa. Stem habit within this taxon ranges from appressed to ascending and a mixture of long-shoots and short-shoots is often found on a single plant. The only characteristic that consistently separates ssp. *adhaerens* from ssp. *deltoidea* on one hand and ssp. *pinetorum* on the other is the occurrence of irregularly twisted hairs in stem pubescence. It differs from ssp. *serpyllum* in having less dense pubescence with only uncinate trichomes on the leaf surfaces. Geographically, ssp. *adhaerens* occupies the area between ssp. *deltoidea* and ssp. *pinetorum* (Figure 1). When trichome length, plant habit, or pubescence density are considered separately, the values found in populations of ssp. *adhaerens* smoothly bridge the gap between ssp. *deltoidea* and ssp. *pinetorum.* Close inspection of Figure 1

suggests that there is an abrupt change in trichome length at the boundary between ssp. *deltoidea* and ssp. *adhaerens,* but specimens with intermediate trichome length exist (*Lakela & Almeda 30450* and *Lakela & Pardue 31583*) that are not mapped because their locations are not accurately known.

The phylogenetic relationships of ssp. *adhaerens* within the complex are not fully clear. Currently, ssp. *adhaerens* is represented by a small series of populations intermediate in morphological features between ssp. *deltoidea* and ssp. *pinetorum.* Also, ssp. *adhaerens* is much more uniform morphologically within populations and has larger differences between populations than the other three taxa of the complex. This pattern of variation suggests that relatively recent hybridization between ssp. *deltoidea* and ssp. *pinetorum* might have given rise to ssp. *adhaerens.* Such a scenario is also supported by the apparent intergradation of ssp. *adhaerens* with those two along its borders. However, hybridization would only be possible if the putative parents were growing in much closer proximity than they are currently. Alternatively, it is possible that the pattern of variation reflects local adaptation to varying environmental factors, such as differences in soil type or water availability. Changes in substrate conditions are at least loosely correlated with the changes in morphological pattern. The range of ssp. *deltoidea* corresponds to that area of the Miami Rock Ridge overlain with a thin layer of white sand (Snyder et al., 1990). The ssp. *adhaerens* occurs in the area with a reddish sandy loam while ssp. *pinetorum* is largely found in the lower, wetter pinelands at the southwestern end of the Miami Rock Ridge. Unfortunately, the pinelands habitat of the complex has been so fragmented and reduced over the past decades that it is no longer possible to make detailed studies to compare these two hypotheses. In particular, the zones where the taxa would have met historically have been obliterated, so the abruptness of the transitions cannot be assessed. It is also possible that the patterns of variation seen in present populations of ssp. *adhaerens* may reflect accidents of preservation more than historical patterns. Despite the uncertainty, I consider the hypothesis of local differentiation more probable on the basis of current evidence.

As noted above, ssp. *adhaerens* does not have the morphological distinctiveness of the other members of the complex. Still, the populations are in most cases easily distinguished from the other taxa and occupy a significant portion of the range of the

complex (Figure 1). The combination proposed by Burch in 1966 (*Chamaesyce deltoidea* ssp. *deltoidea* var. *adhaerens*) does not adequately describe the position of ssp. *adhaerens* within the complex. In particular, there is no reason to believe that ssp. *adhaerens* is more closely related to ssp. *deltoidea* than it is to ssp. *pinetorum*. For these reasons, and in accordance with the hypothesis that the various morphological types all arose independently through adaptation to local conditions, I use the rank of subspecies for all taxa in the complex.

## TAXONOMIC TREATMENT

**Chamaesyce deltoidea** (Engelmann ex Chapman) Small

Plants herbaceous, stems 10–15 cm long, wiry, radiating from a woody taproot, appressed to the ground surface or ascending to erect. Leaves reniform to ovate; thick, obscuring secondary venation; bases strongly inequilateral, commonly shallowly cordate; margins entire, thickened, usually inrolled. Stipules membranaceous; usually joined to base and deltoid in outline, often lacerate or lobed, sometimes split fully to the base; white to reddish; inconspicuous. Inflorescences solitary in leaf axils. Peduncle shorter than to slightly exceeding the leaf. Cyathia glabrous to densely pubescent, involucre campanulate, .9 to 1.9 mm long, .5 to 1.7 mm wide, lobes triangular, equalling to slightly exceeding the glands. Glands elliptic, .4 mm long, .3 mm wide. Gland appendages minute or lacking. Capsule glabrous to densely pubescent, about 1.3 mm long. Seeds about 1 mm long, quadrate, brown, the flat surfaces usually having 3–4 shallow (sometimes inconspicuous) ridges.

## KEY TO SUBSPECIFIC TAXA OF *CHAMAESYCE DELTOIDEA*

1. Stems erect or ascending
   2. Pubescence of leaves spreading, .6–.7 mm long, straight; pubescence of stems same . . . . . **3.** ssp. *pinetorum*
   2. Pubescence of leaves appressed, .1–.25 mm long; pubescence of stem spreading or ascending, .1–.25 mm long, irregularly twisted . . . . . **2.** ssp. *adhaerens*
1. Stems prostrate or appressed to ground surface
   3. Pubescence of leaves sparse, appressed; stems glabrous or thinly pubescent; hairs on leaves uncinate; hairs on stems uncinate . . . . . **1.** ssp. *deltoidea*

3. Pubescence of leaves dense, appressed to spreading; pubescence of stems dense; hairs on leaves uncinate or irregularly twisted; hairs on stems irregularly twisted
4. Pubescence of leaves composed of irregularly twisted hairs; plants appearing silver or gray . . . . . **4. ssp. *serpyllum***
4. Pubescence of leaves uncinate; plants bright green . . . . . **2. ssp. *adhaerens***

1. **Chamaesyce deltoidea** (Engelmann ex Chapman) Small ssp. **deltoidea**, Fl. Southeastern U.S., p. 710, 1903.

*Euphorbia deltoidea* Engelmann ex Chapman, Flora of the Southern U.S., ed. 2, p. 647, 1883. TYPE: United States. Florida [Dade Co.], rocky pine woods, Bay Biscayne, June, *Curtiss 2474** (LECTOTYPE: MO (1792963)! (herein designated); ISOTYPES: CU!, GH!, MIN!, NCBS!, NY [3 sheets]!, PH [2 sheets]!, US [2 sheets]!)

Plants forming small mats with stems and leaves appressed to ground surface, bright green. Margins of adjacent leaves on most stems typically overlapping. Stems glabrous or very sparsely pubescent with appressed, uncinate trichomes .10–.25 mm in length. Leaves usually glabrous above, often sparsely pubescent beneath with appressed, uncinate trichomes .10–.25 mm in length. Cyathia and capsules glabrous to sparsely pubescent.

Although Chapman credited Engelmann with this species, comparison of the published description (Chapman, 1883) with the specimen in the Engelmann herbarium (MO 1792963) and with a manuscript description by Engelmann (MO archives, Engelmann collection), shows that Chapman's description was derived independently. The Engelmann name was known to Chapman from one or more specimens in the exsiccata series North American Plants distributed by A. H. Curtiss (*Curtiss 2474**). All replicates of *Curtiss 2474** that could be located in this country were examined, but none was found that could be identified with the specimen Chapman used in drawing up his description. Burch annotated the specimen in the Engelmann herbarium as lectotype for the species, and I accept this choice. The remaining replicates of *Curtiss 2474** have traditionally been treated as isotypes. Exsiccata numbers in this series are not equivalent to collection numbers, but * and ** are appended to exsiccata numbers elsewhere in the series to denote different collections of the same species.

Also, specimens of *Curtiss 2474** I have seen are consistent with replicates from a single gathering, so I acccept them as isotypes. The year of collection of *Curtiss 2474** remains uncertain, but annotations on sheets received by Engelmann and the U.S. Department of Agriculture suggest that the specimens were collected in 1880.

This is the most northerly taxon in the complex. Its historical range was in the dry Miami Rock Ridge Pinelands from about the center of Miami to some 13 miles south. All but a few remnants of this pineland area have been converted to commerical or residential use. In those remnants, the *Chamaesyce* grows in a thin layer of white sand over limestone bedrock. It is most abundant in areas free of shrubby undergrowth. Most of the remaining populations are found on lands owned by the federal, state or local governments, and, given protection from development as well as periodic burns to keep the pinelands open, should persist indefinitely. Management regimes imposed in these pineland remnants, however, could affect survival of the populations in unforeseeable ways. Continued population monitoring will be necessary to provide sufficient warning of potential adverse effects.

REPRESENTATIVE SPECIMENS: UNITED STATES. **Florida:** Dade Co., pinelands north of Goulds, 10 Aug 1963, *Burch 144a* (FLAS, MO, NY); rocky pine woods near Miami, 11 July 1895, *Curtiss 5468* (F, FLAS, GH, MIN, NY, US); Miami, July 1877, *Garber sn* (F, FLAS [2 sheets], GH, NY, US [2 sheets]); in dry sandy pineland, Buena Vista, 26 Dec 1929, *Moldenke 291* (MO, NY, PH, US); Miami, 13 May 1904, *Tracy 9114* (CU, F, GH, MIN, MO, NY, PH, US).

2. **Chamaesyce deltoidea** ssp. **adhaerens** (Small) Herndon, *comb. et stat. nov.*

*Chamaesyce adhaerens* Small, Torreya 27: 104. 1927. TYPE: United States. Florida, Dade Co., pinelands between Peters Prairie and Homestead, 10 Nov 1906, *Small & Carter 2531* (HOLOTYPE: NY!).

Stems and leaves appressed to ground surface and plants forming small mats or stems ascending and plants forming small tufts. Margins of adjacent leaves on most stems overlapping. Stems pubescent with ascending to spreading, irregularly bent trichomes .25–.55 mm in length. Leaf trichomes nearly the same length but appressed, uncinate.

As discussed in the text, this taxon occupies the gap between

ssp. *deltoidea* and ssp. *pinetorum* both geographically and morphologically. It is found in the Redlands area of Dade Co. where it grows on a fine, reddish sandy loam over limestone bedrock in remnants of the Miami Rock Ridge Pinelands. It is the rarest taxon in the complex, and the one most likely to be lost because no known populations are found on protected lands.

REPRESENTATIVE SPECIMENS: UNITED STATES. **Florida:** Dade Co., badly burned pinelands on south side of Bauer Dr., east of Krome Ave., 3 May 1978, *Avery 1884* (Everglades National Park, FLAS, USF); open pineland near Homestead, 16 Apr 1964, *Burch & Ward 271* (F, GH, MO); open pine-palmetto forest, Homestead, 9 Aug 1980, *Herndon 402* (FLAS, FTG; also distributed to JBSD, NCU, TEX, US); Pinelands, near Murden Hammock, 22 June 1915, *Small, Mosier & Small 6451* (FLAS, GH, NY).

3. **Chamaesyce deltoidea** ssp. **pinetorum** (Small) Herndon, *comb. et stat. nov.*

*Chamaesyce pinetorum* Small, Bull. N.Y. Bot. Gard. 3: 4. 1905. TYPE: United States. Florida, Dade Co., Pinelands near the homestead road, between Cutler and Longview Camp, 9–12 Nov 1903, *Small & Carter 836* (HOLOTYPE: NY!; ISOTYPE: PH!). *Euphorbia smallii* Oudejans, Phytologia 67: 236, 1989.

Plants forming small tufts. Stems ascending to erect, usually red. Margins of adjacent leaves on most stems not overlapping. Stems, leaves, and capsules villous, with straight, spreading trichomes .6–.7 mm in length.

In addition to the easily identified holotype and isotype, there are a few more potential isotypes which should be noted. These specimens have the same label data as *Small & Carter 836,* but do not have a collection number. One such sheet at US was annotated as an isotype by Burch.

Strongly upright, often red stems give this plant a highly distinctive appearance. It grows in rarely flooded pinelands, although it seems to grow in slightly wetter areas than the other three taxa. This subspecies is currently the most abundant of the complex, primarily because almost a quarter of its original range falls within the boundaries of Everglades National Park. It is protected from direct habitat destruction, but its survival may be dependent upon the specific fire regime imposed.

REPRESENTATIVE SPECIMENS: UNITED STATES. **Florida:** Dade Co., pinelands near Long Prairie, 24 Mar 1904, *Britton 193* (F, NY); open pine wood, Princeton, 30 Nov 1963, *Burch 232* (FLAS, NY, US); open rocky pinelands, Homestead, 13

Apr 1980, *Herndon 348* (FTG; also distributed to JBSD, NCU, RSA, TEX); open rocky pinelands, Long Pine Key, Everglades National Park, 5 Jun 1981, *Herndon 514* (FLAS, FTG; also distributed to JBSD, NCU, RSA, TEX); Pinelands about Sykes Hammock, 2 Jul 1915, *Small, Mosier & Small 6761* (FLAS, GH, NY).

4. **Chamaesyce deltoidea** ssp. **serpyllum** (Small) Burch, Ann. Missouri Bot. Gard. 53: 90–99, 1966.

*Chamaesyce serpyllum* Small, Flora Florida Keys 81. 1913. TYPE: United States. Florida, Monroe Co., Big Pine Key, 17 Nov 1912, *Small 3811* (HOLOTYPE: NY!). *Euphorbia deltoidea* Engelmann ex Chapman var. *serpyllum* (Small) Oudejans, Phytologia 67: 45, 1989.

Stems and leaves appressed to ground surface, forming small silver-green to white mats. Margins of adjacent leaves on most stems not overlapping. Stems, leaves and capsules densely pubescent with appressed to ascending, irregularly bent trichomes .1–.25 mm in length.

The dense, silvery pubescence of this plant blends in amazingly well with the surface of the coral rock it grows on and probably also provides considerable protection against desiccation in the hot, dry pinelands of the lower Florida Keys.

Much of the original range of this subspecies lies within the boundaries of the National Key Deer Refuge and is protected from direct habitat destruction. Continued commercial and residential development in the Florida Keys, however, could adversely affect the subspecies through changes in availability of fresh water or changes in fire regime. Currently, the subspecies is widespread in the pineland areas of Big Pine Key, but the populations are scattered, and the total number of plants does not appear to be large.

REPRESENTATIVE SPECIMENS: UNITED STATES. **Florida:** Monroe Co., occasional in pine woods, Big Pine Key, 10 Aug 1963, *Burch 139* (FLAS, GH [2 sheets], MO, NY); Big Pine Key, 8 Feb 1977, *Correll & Popenoe 48057* (FTG, NY); pine woods, Big Pine Key, 1–17 Feb 1937, *Killip 32062* (GH, MO, US); Pinelands, Big Pine Key, 12 Nov 1912, *Small 3768* (F, NY [2 sheets]); Pinelands, Big Pine Key, 17 Dec 1913, *Small & Small 5027* (F, NY).

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# THE INTERPLAY OF BOTANISTS AND *POTENTILLA ROBBINSIANA*: DISCOVERY, SYSTEMATICS, COLLECTION, AND STEWARDSHIP OF A RARE SPECIES

CHARLES V. COGBILL

## ABSTRACT

*Potentilla robbinsiana* Oakes ex Rydb. was first collected ca. 1824 by Thomas Nuttall on Monroe Flats in the Presidential Range of New Hampshire. Partly because the plant has always been rare, botanists have searched for, collected, studied, hiked past, propagated, and protected it. This paper documents botanical exploration, taxonomic interpretations, and historical status of *P. robbinsiana* populations. In the last 160 years, human interplay with *P. robbinsiana* has gone through roughly three phases of intense interest: discovery, collection and stewardship. In each period, human perceptions of, and reactions to, the rarity of this species have changed. The most significant human impact on the Monroe Flats plants was trail disturbance and zealous herbarium collection in the late 1800's. Even the cumulative removal of over 850 plants (equivalent to approximately half of the population) has not permanently affected the population size or distribution on Monroe Flats. Active conservation over the past 75 years has supplemented the natural resilience of the species. A second tiny and imperiled population on Franconia Ridge, discovered by Edward Tuckerman, Jr. ca. 1840, has never drawn much management or botanical interest.

Key Words: *Potentilla robbinsiana*, historical ecology, conservation biology, endangered species, alpine zone, herbarium collections, Thomas Nuttall, William Oakes, Edward Tuckerman, Jr., White Mountains, New Hampshire

## INTRODUCTION

*Potentilla robbinsiana* Oakes ex Rydb. (dwarf cinquefoil), the only plant species endemic to the White Mountains of New Hampshire, is singularly relict. It has persisted—perhaps at only two spots—since the alpine region was separated from the arctic some 9000 years ago (Spear, 1989). The nearest related species, *Potentilla hyparctica* Malte (Löve and Löve, 1965, 1966), occurs 600 km to the north at four sites in the western Shickshock Mountains of the Gaspé, Québec, Canada. The latter alpine plants are themselves equally isolated, 800 km from arctic populations (Hultén, 1968).

Native *Potentilla robbinsiana* presently grows in two restricted locations. The primary population of 1500–2000 flowering individuals occurs on Monroe Flats (Sargent's Purchase, Coos

County), 2 km southwest of the summit of Mount Washington and just south of Lakes of the Clouds. The area (1548 m elevation) is at the head of Oakes Gulf, just above treeline in the col between Mt. Monroe to the west and the south shoulder (Bigelow Lawn) of Mount Washington to the east. Here a low dome of till supports the most well-developed turf-banked terraces in the White Mountains. Most *P. robbinsiana* plants grow on the periphery of this knoll, primarily southeast of the barren crown. Some 30 km to the west, a second tiny population is found in the small alpine zone on Franconia Ridge (Franconia, Grafton County). This station of less than ten individuals is on a west-facing cliff (1460 m elevation) just south of Mt. Lincoln.

*Potentilla robbinsiana* was listed as federally endangered in 1980 (Cook, 1980). Although a "classic rarity," with both highly restricted geographic range and habitat specificity (Rabinowitz, 1981), the species is locally abundant at one locality and occurs in a distinctly different habitat at a second (Graber, 1980; Fitzgerald et al., 1990). Further dimensions of *P. robbinsiana*'s rarity include close human contact and taxonomic ambiguity. Despite recent population studies and political concern (Steele, 1964; Graber, 1980; Graber and Brewer, 1985; Fitzgerald et al., 1990), the botanical history of *P. robbinsiana* has been little known except for herbarium collections.

## Herbarium Collections

Herbaria provide an unparalleled database on historic collection locations, collector activity, and taxonomic treatment. Of the 96 public herbaria contacted for information on *Potentilla robbinsiana* and its synonyms, 59% (57) had some plant material (Table 1). Specimens are found today in herbaria from St. Johnsbury, Vermont to Grahamstown, South Africa. Herbaria typically contain massive collections from the late 19th century. Although large New England herbaria have traditionally been tapped for local information, they contain less than 20% of the more than 235 existing sheets of *P. robbinsiana*. Previous studies using 21 to 50 sheets (Pease, 1924; Steele, 1964; Graber, 1980; New Hampshire Natural Heritage Inventory files) have given a limited picture of collection history. Significantly, most early and most Franconia collections are found in European herbaria.

The extensive herbarium material represents one of the most

Table 1. Number of separately labelled collections of *Potentilla robbinsiana* known from various public herbaria.

| | Monroe Flats | | | Franconia | | | |
|---|---|---|---|---|---|---|---|
| Location | 1824– | 1858– | 1916– | 1840– | Total | Sheets | Plants |
| Herbaria | 47 | 1909 | 83 | 1915 | (#) | (#) | (#) |
| Large New England (GH, NEBC, HNH, NHA, VT) | 8 | 49 | 1 | 2 | 60 | 42 | 220 |
| Other New England (in 10 of 15 checked) | 9 | 27 | 6 | 2 | 44 | 41 | 135 |
| Large American (US, NY, PH, F, MO, CAN) | 5 | 54 | 3 | 3 | 65 | 56 | 210 |
| Other American (in 19/42) | 2 | 57 | 7 | 1 | 67 | 61 | 201 |
| Outside N. America (in 17/28) | 28 | 6 | 4 | 5 | 43 | 35 | 113 |
| All known ($n$ = 57/96) | 52 | 193 | 21 | 13 | 279 | 235 | 879 |

intensive collections of a single species yet documented. It is even more impressive considering most collections are from a single site. Herbaria contain 279 separate labels of 879 individual plants collected from ca. 1824 to 1983 (Table 1). Forty-eight collectors are represented, but over half of the plants were taken by only six botanists (W. Oakes—20 sheets; E. Tuckerman, Jr.—23 sheets; C. G. Pringle—28 sheets; Faxon brothers—17 sheets; W. W. Eggleston—55 sheets; and E. F. Williams—13 sheets). In addition, many specimens were not deposited (e.g., are in personal herbaria, used for transplants or cultivation, or lost). Since the 846 known specimens collected at Monroe Flats represent a minimum number, it is probable that collectors have removed well over a thousand plants.

## DISCOVERY

The dates, locations, nomenclature, and even origin of most early reports of *Potentilla robbinsiana* are unclear. Conflicting accounts credit at least five botanists, in addition to Robbins, with its discovery. The original publication of *Potentilla robbinsiana* cites material from "Nuttall! Oakes! Tuckerman!" (Torrey and Gray, 1840). While Thomas Nuttall apparently collected it in 1824, the earliest dated herbarium specimen (UPS) is from William Oakes and Charles Pickering in 1825. In 1840, Edward

Tuckerman, Jr. wrote that "Mr. Oakes who discovered it at this station had it only in fr[uit]" (CuCo 3/1840). In a letter written in October 1840, Tuckerman acknowledged that both Nuttall and Oakes "had only previously found the plant," but intriguingly added that "Mr. Greene had also found it" (QK). Benjamin D. Greene was at Lakes of the Clouds in 1823 when he found at least two other rare species (Pease, 1917, 1964), but *P. robbinsiana* is notably absent from Greene's collections cited in Bigelow (1824). Without a specimen, field notes or substantiating account, any reports before 1824 are uncertain.

**Thomas Nuttall**

Either Asa Gray or John Torrey had "seen an authentic specimen" of *Potentilla robbinsiana* from Nuttall. Retaining chronological priority, they listed Nuttall first (Torrey and Gray, 1840). Although no dated material survives, Thomas Nuttall almost certainly collected *Potentilla robbinsiana* in August 1824. Notes on herbarium sheets of *P. robbinsiana* indicate that in September 1839, Nuttall told Edward Tuckerman, Jr., "that he also found it" (UPS, QK). Charles Pickering (1879) even wrote that in 1824 "Nuttall [was] visiting the White mountains, meeting with . . . on the alpine portion of the mountains, *Potentilla frigida* [= *P. robbinsiana*], *Gnaphalium supinum* . . . and *Salix repens.*" Nuttall made only one trip to the White Mountains, obviously collecting alpine plants in August 1824 when he signed Crawford's register (CrPa, 12/8/1824; Pease, 1918; Graustein, 1967). A sheet of *S. uva-ursi* (= "*S. repens*") from Nuttall's herbarium (BM) is indeed labeled "White Mts., 1824. . ." There are no collections of *P. robbinsiana* now in Nuttall's herbarium, but one undated specimen of "*Potentilla brauniana* Hoppe" from the "White Mountains" attributed to Nuttall is in Hooker's herbarium at Kew. This sheet (K) thus appears to be part of Nuttall's original collection and the earliest surviving collection of *Potentilla robbinsiana.*

William Oakes was competitive and thus skeptical of Nuttall's rarities. He referred to *Gnaphalium supinum* as "Nuttall's doubtful" species (OaCoGH, 4/1829) and summarily dismissed Nuttall's *Carex atrata* as variously misidentified (e.g., TuPa, 8/1839). Apparently in reaction to Torrey's publication acknowledging Nuttall's collections, Oakes wrote to Torrey that Nuttall had told him that Nuttall ". . . did not find them [*Potentilla minima* and *Arnica mollis*] himself." Oakes asserted that "Nuttall's specimens

. . . were given him . . . by Dr. Holmes of Maine, who was posterior to P[ickering] and myself . . .” (ToCo, 4/1841). In fact, Ezekiel Holmes' only known trip to Monroe Flats was on 27 July 1825, when he “coasted along by blue pond and Mt. Monroe . . .” in the company of Oakes (CrPa, 7/1825). Confusingly Oakes must have been responsible for any collection by the young Holmes. It seems likely that Oakes' self-serving story was simply trying to obfuscate the discovery of *P. robbinsiana* by the reticent Nuttall (cf. Graustein, 1964, 1967).

**William Oakes**

The major early collections of *Potentilla robbinsiana* are attributed to William Oakes. During several weeks in 1825 Oakes made “tours around the mountains” collecting “some rare [plants] . . . not to be found elsewhere in America” (Crawford, 1846). Oakes, together with Charles Pickering, made collections of a dozen new alpine species (Oakes, 1841; Pickering, 1879; Pease, 1964). They apparently found *P. robbinsiana* at this time, as the only dated herbarium sheet was collected by “Pickering & Oakes, July 1825” (UPS).

In 1827 both Oakes and Pickering returned to Ethan Crawford's house (CrPa, 18–28/7/1827). Oakes collected *Potentilla robbinsiana* in July 1827, as he wrote to John Torrey that he had “just returned from the White mountains and had found 3 more flowering specimens of the little Potentilla . . . [with] several hundred specimens observed” (ToCo, 8/1827). In addition, Tuckerman stated (UPS) that Oakes and Pickering found *P. robbinsiana* in 1827 and a collection (QK) attributed to Pickering alone must be from either 1825 or 1827 (Pickering, 1879; Pease, 1964). In April 1828, Oakes sent Torrey one flowering specimen of “*Potentilla frigida*” (ToCo, 15/4/1828). A single specimen in a small packet labeled “*Potentilla frigida,* Vill., Wh. Mts., Oakes” (NY) fits this description and is apparently contemporary, albeit not obtained directly from Torrey's herbarium.

**Other Early Collections**

Before its first published mention in 1840, *Potentilla robbinsiana* was known by many. In 1829, Ethan Crawford helped “some

botanists from Boston . . . [collect] an assortment . . . [of] delicate mountain flowers" to send to Europe (Crawford, 1846). These plants probably included *P. robbinsiana* (PR) and the type of *Prenanthes bootii* (G; Pease, 1917; Graustein, 1964) collected by J. W. Boott in 1829, as well as the *P. robbinsiana* (PR) attributed to Francis Boott's herbarium (Lehmann, 1851). Oakes and Tuckerman both made multiple collections of *P. robbinsiana,* and at least four other botanists had herbarium collections by 1840.

Some of Oakes' collections come from his later explorations, 1843–47 (Pease, 1964). For example, two fruiting specimens, "Legit Oakes" (NY), are from the Princeton (perhaps Torrey's) herbarium, and the nomenclature "*Potentilla minima*" dates them in the 1840's. Oakes certainly got *P. robbinsiana* in 1843 when he collected all known rare species in the White Mountains (Pease, 1917). In 1844, Oakes first discovered *Euphrasia oakesii* at an unknown location, but probably on Monroe Flats where it has always grown together with *P. robbinsiana* (Oakes, 1847; Robinson, 1901).

Despite contemporary knowledge of Nuttall's, Oakes' and Boott's early collections, they were later overlooked. For example, Asa Gray (1867) only cited collections attributed to "Robbins, Tuckerman, & c. . . ." Following Gray, researchers (e.g., Allen, 1888; Rydberg, 1898; Fernald, 1950; Graber, 1980; Lanier and Hill, 1983) have erroneously believed that James W. Robbins discovered *Potentilla robbinsiana.* In 1829 William Oakes, the source for the specific name, sent Robbins on a highly successful collecting trip to the White Mountains (Oakes, 1841; Pease, 1917). Although Oakes had mailed him a specimen of *P. robbinsiana* in April 1829 (OaCoGH, 4/1829) and "directed him exactly . . . [to] the locality of the rarer plants[,] . . . Robbins found none of [them]" (TuCo, 4/1841). Neither herbarium sheets nor any report of *P. robbinsiana* by Robbins has been found. Ironically, it appears that Robbins was one of the few botanists who visited the area before 1830 who did not collect his namesake. Furthermore, the possessive form of the colloquial name, Robbins' (sic) cinquefoil, is a misnomer. The Latin adjectival suffix (-iana) implies that Robbins was simply being complimented (Stern, 1966). Although he admittedly did "not care much for the Lindley rule" (TuCo, 12/1843), Oakes clearly recognized discoverers with a genitive (-ii suffix) specific epithet.

**Locale of First Collections**

Until 1840, *Potentilla robbinsiana*'s location was "obscure & out of the way of travellers" (CuCo 3/1840). No *P. robbinsiana* collected before 1839 bears an exact location, but circumstantial evidence indicates that all came from Monroe Flats. Early explorers (e.g., Bigelow and F. Boott in 1816) used an eastern route up the White Mountains (OaCoAAS, 10/1844), and none reported *P. robbinsiana.* Collections apparently started only after the first Crawford Path was cleared on the west side in 1819 (Crawford, 1846). This route passed near Mt. Monroe, but after 1821 most trips up Mount Washington were made over a more northerly second Crawford Path (Waterman and Waterman, 1989). The latter route was a "poor one for botanizing" (Southwick, 1842), and botanists obviously explored interesting areas near "E. A. Crawford's old path" (Oakes, 1841). Both Nuttall and Oakes visited the Monroe region well before a bridle path first crossed Monroe Flats ca. 1840 (Waterman and Waterman, 1989). In 1824 Nuttall found *Gnaphalium supinum* in a "dry ravine of the Amonoosuck" (Torrey and Gray, 1840), conceivably the edge of Monroe Flats. Similarly, Nuttall's collection of the rare *Carex atrata* (Beck, 1833) is consistent with a site near Oakes Gulf. In 1825, Oakes first visited the "fertile locality" of Oakes Gulf (Pease, 1917). All of Oakes' sheets in 14 herbaria are simply from "Alpine Region, White Mountains, New Hampshire," but Tuckerman definitively states that Oakes found *P. robbinsiana* at only one station (CuCo 3/1840; QK). Significantly, Tuckerman wrote that *P. robbinsiana* was found "by Mr Oakes & Dr. Pickering at the same station where I found it" (UPS). This location, unquestionably Monroe Flats, was the "peculiar home of the alpine cinquefoil" (Tuckerman, 1860).

The flora of the Franconia Range was "very poor" (OaCoAAS, 10/1844), but *Potentilla robbinsiana* was found there at first exploration. Although the new site was never publicized, Edward Tuckerman, Jr. collected five undated herbarium sheets (7 specimens) from the "Franconia Mountains" (NY, K, UPS, E). One sheet (UPS) elucidates the location as "Great Haystack" where Tuckerman first recorded alpine species in 1840 (TuCo, 10/1840; Tuckerman, 1843). Tuckerman was distributing *P. robbinsiana* in Europe in 1841–42 where most of his Franconia specimens are now found. In the late summer of 1844, Tuckerman returned to

Franconia Ridge for a "very thorough exploration of the Gt. Haystack." He then stated that "*Potentilla* (*minima*) is limited to the spot where I first found it & here only grows *Polygonum vivip.* . . ." (OaCoAAS, 10/1844). Thus his Franconia discovery was presumably ca. 1840 from a single station. Interestingly, Tuckerman's collection of *Polygonum viviparum* (NY) was the only time this species has ever been recorded from Franconia.

## SYSTEMATICS

### Early Taxonomic Uncertainty

Early American botanists were initially confused about the taxon to which their alpine *Potentilla* belonged. Without an American counterpart, most early collections of the dwarf *Potentilla* from the White Mountains were compared to various European taxa. For example, Nuttall's ca. 1824 specimen (K) is labeled "*P. Brauniana*"; F. Boott's 1829 plant (PR; Lehmann, 1851) has the undeterminate "*Pot.* sp." annotated to *P. nivea?*; and J. W. Boott's 1829 companion collection (PR) is identified as *P. villosa.* While there was some early agreement that the plants belonged to *P. brauniana,* Oakes initially decided it belonged to another European alpine species. In 1827, Oakes simply called it the "little Potentilla" and stated that the specific taxon "cannot be settled until European botanists will make up their minds" (ToCo, 8/1827). Soon afterward, Oakes called it "*Potentilla frigida*" when he sent specimens to John Torrey (ToCo, 4/1828). Ironically, Torrey's reply asked if Oakes was "convinced that this cannot be the species we first considered it (*P. nana* Lehm.)" (OaCoAAS, 4/1828). Prophetically, Torrey's early determination placed it with the then little known arctic species to which it is now considered most closely related.

Early collectors had trouble recognizing the species without a name or description, yet taxonomists were dependent on their collections. For instance, Tuckerman was still unaware of *Potentilla robbinsiana* 15 years after its discovery and he failed to recognize it as he first crossed Monroe Flats. In June 1839 he collected a "Pl[anta] incog[nita] near snow Mt. Monroe" (TuPa, 24/6/1839). Two days later, he refined his identification of the unknown plant to "Planta Rosacearum." Later that summer, Tuckerman had identified the rose's genus (TuPa, 8/1839), and

specifically discussed the *Potentilla* collections and taxonomy with both Oakes and Nuttall. After an evening talk with Oakes, Tuckerman recorded their uncertainty: "*Potentilla* −−− Mr Oakes doubtful about" (TuPa, 2/8/1839). Oakes, nevertheless, must have developed the idea of a distinct species, as two weeks later Tuckerman annotated a specimen collected earlier that summer: "*Potentilla Robbinsiana* Oakes! MSS." (NEBC). In September 1839, Nuttall also told Tuckerman that he still "considered it distance [sic] from *P. Brauniana* or *P. verna* or *nivea*" (UPS).

Although Oakes coined the name "*Robbinsiana*," he never published a description and apparently only communicated the name privately. The first published description of the taxon listed "*Potentilla Robbinsiana,* Oakes! mss." as a synonym for an unnamed variety of the species *P. minima* (Torrey and Gray, 1840). Significantly, one 1825 collection by Oakes has an original label with the same nomenclature: "*Potentilla Robbinsiana* Oakes MSS." (UPS). All Oakes' other specimens or manuscript material referring to "*Robbinsiana*" have apparently been relabeled or lost. Confusingly, most of Oakes' herbarium sheets have printed labels with *Potentilla minima* and *P. Robbinsii* (sic) as a synonym. These labels, however, were added by Asa Gray after Oakes' death in 1848 (Gray, 1849). They were part of sets of "most of the rarer plants found in New England" which were sold (at $20 per 500 species) accounting for the wide distribution of Oakes' herbarium. Significantly, Oakes seldom, if ever, wrote the name "*Robbinsiana*" himself, rather choosing "*frigida*" on both surviving herbarium material and correspondence before 1840 (e.g., NY; ToCo, 3/4/1828; OaCoGH, 4/1829). After Torrey and Gray submerged *P. Robbinsiana* under *P. minima,* Oakes changed his designation and refered to the species as "*Potentilla minima*" (e.g., ToCo, 4/1841; TuCo, 12/1843). Curiously, even after receiving credit for the species name *Robbinsiana,* Oakes rejected it.

## Taxonomic Revision

The long lack of recognition, due in part to confused taxonomy, was finally settled by Asa Gray. Working on the Roseaceae for Torrey's *Flora of North America* in the 1830's, Gray examined *Potentilla* material, including Lehmann's herbarium (GrCo, 10/1839; Torrey and Gray, 1840). Torrey and Gray (1840) decided that the White Mountains species "agrees well with the character

of *P. minima*" Haller, the accepted synonym of *Potentilla braunniana* Hoppe (Koch, 1837). They relegated "*P. Robbinsiana*" to a variety (Torrey and Gray, 1840). Interestingly, Gray only saw plants in the field in September 1842, while on a trip with Tuckerman (GH, OXF). The first edition of Gray's Manual (1848) continued to recognize *P. minima* with the short-stemmed, small-flowered American variety. Although *Potentilla* expert Lehmann (1851) concurred exactly with this designation, Gray (1856) later transferred the taxon to *P. frigida* Villars. After being accepted as a variety of various European species for over 70 years, *P. robbinsiana* was validly given full species status by Rydberg (1896). Others (e.g., Britton and Brown, 1897; Rydberg, 1898; Wolf, 1908; Robinson and Fernald, 1908) concurred with this determination.

The genus *Potentilla* is known for its "devilish combination of apomixis, hybridization, and morphological plasticity" (Polunin, 1959). Due in part to the obscure evolutionary history of this "anomalous species" (Fernald, 1950), the taxonomic status of *P. robbinsiana* is still unclear (e.g., Fernald, 1931; Löve and Löve, 1965, 1966). One chromosome count from Monroe Flats showed an odd number polyploid $2n = 49$, which would indicate an obligate apomict (Löve and Löve, 1966). *Potentilla robbinsiana* is indeed agamospermous (T. D. Lee, pers. comm.). Although Löve and Löve (1966) concluded that *P. robbinsiana* "is apparently an apomictic segregate of *Potentilla hyparctica,*" the taxon could also be a hybrid conserved by apomixis (Steele, 1964). *Potentilla hyparctica* itself is not well defined, but is typically $2n = 42$ (Malte, 1934; Löve and Löve, 1965; Dansereau and Steiner, 1956; Fernald, 1943; Moore, 1982). A distinct ancient hybrid between *P. hyparctica* and a $2n = 56$ taxon (known in other arctic species in the genus) producing the $2n = 49$ Monroe Flats' plant seems plausible. While being related to *P. hyparctica* (Löve and Löve, 1965, 1966; Crow, 1982), this hybrid would explain the enigmatic nature of *P. robbinsiana.*

*Potentilla robbinsiana* is morphologically distinctive, probably a direct result of its limited genetic variability. For example, flowering stem lengths of plants from the White Mountains overlap only slightly with those of *P. hyparctica* (Table 2). Even alpine *P. hyparctica* from the Gaspé can be easily distinguished from the White Mountain population (Fernald, 1950; D. Marris, MT herbarium note 1972). When grown in the greenhouse, however, Monroe Flats plants take on some of the characteristics of their

Table 2. Measurements of fruiting stem length from late-July and August herbarium collections of *Potentilla* from the White Mountains, New Hampshire, the mountains of the Gaspé and the low arctic in Québec, Canada.

| Location/ Collection | Plants measured (*n*) | Fruiting stem length (mm) | | |
|---|---|---|---|---|
| | | Mean* | ±SD | Range |
| Monroe Flats | | | | |
| Nuttall ca. 1824 | 1 | 18.10 | | 18.1 |
| Oakes pre-1848 | 19 | 16.74b | 5.61 | 7.2–26.5 |
| Tuckerman ca. 1840 | 11 | 22.91a | 6.42 | 13.1–33.1 |
| Since 1880 | 194 | 22.74a | 5.88 | 6.3–39.6 |
| Franconia | | | | |
| Tuckerman ca. 1840 | 6 | 45.38c | 11.65 | 26.0–57.7 |
| North 1897–1908 | 2 | 18.50 | 8.34 | 12.6–24.4 |
| Fernald 1915 | 17 | 20.30a | 4.09 | 13.1–26.2 |
| Québec (*P. hyparctica*) | | | | |
| Gaspé | 37 | 69.53d | 22.95 | 35.1–103.7 |
| Ungava | 24 | 68.26d | 20.78 | 31.8–123.7 |

* Different letters indicate a significant (*t*-test, $P < .05$) difference between means.

arctic relatives (Löve and Löve, 1965; K. D. Kimball, pers. comm.). Nevertheless, the geographic isolation, morphological differences, narrow ecological range and asexual breeding system all argue for the continued species-level separation of *P. robbinsiana.*

Collections from the Franconia Range in the 1840's are different from either Monroe Flats or recent Franconia plants. Their habitat, presumably damp mats with *Polygonum,* was also odd. Tuckerman labeled the specimens "*forma aestivalis*" and on one sheet indicated the character of "*pedunc. elongatis*" (NY). Long fruiting stems (unfortunately there are no flowers), place them between *P. robbinsiana* and *P. hyparctica* (Table 2). These remarkably different plants perhaps represented genetically distinct stock.

## PRESENT DISTRIBUTION

### Population on Monroe Flats

In 1839 *Potentilla robbinsiana* was found on a "stony alpine moor on Mount Monroe" (TuPa, 6/1839; Tuckerman, 1843). Its distribution was then described as "very limited & very [struck out] obscure" (CuCo 3/1840). Since 1865, herbarium records

have cited it as specifically along the Crawford Path (GH). The original Crawford Path skirted the southeast edge of the knoll within the upper edge of the present range of *P. robbinsiana* (Figure 1). Reminiscences from the 1960's also place the majority of the *P. robbinsiana* plants on the southeast side of the knoll and figuratively "moving toward" the outcrop (C. Harris, pers. comm.). A survey of this main population in 1967 revealed a distribution east of the trail, very similar to the present range (W. N. Tiffney, Jr. and B. K. Fowler, pers. comm.). The .11 ha area occupied by the main population has changed little from 1973 to the present (Graber, 1980; Graber and Brewer, 1985; Figure 1).

In addition to the main congregation of *Potentilla robbinsiana* near the rock outcrop at the south edge of knoll, there has been a handful of small outlier populations on Monroe Flats (Figure 1). These sub-populations, scattered over the .85 ha barren area, are in marginal habitats and may be ephemeral. Currently, three peripheral populations, all "discovered" since 1983, are scattered to the north of the main population. In 1985, these outliers had a total of 15 flowering individuals; this number decreased to nine plants in 1992.

For over 40 years, a notable outlier population was found west of the post-1918 Crawford Path. About 1900, *Potentilla robbinsiana* grew there "in dry stony soil" together with *Euphrasia oakesii* (Robinson, 1901). In 1946, Steele (herbarium notes) still found both species "on the southwestern side of a shaly hump." This *P. robbinsiana* sub-population contained a limited number of plants (i.e., 12 to 50 individuals as estimated by F. Steele, C. Harris, W. N. Tiffney, Jr.) and was last seen about 1969. Interestingly, the only extant colonies of *Euphrasia* are now east of the trail just beyond *Potentilla*'s range; apparently both of these species have been extirpated from the west side of Monroe Flats. Steele's often-quoted conclusion (e.g., Cook, 1980; Graber, 1980; Lanier and Hill, 1983) that *P. robbinsiana* now occupies one-fourth of its 1934 area is based on the disappearance of the restricted sub-population west of the trail (Steele, personal herbarium notes, 1977). A colony 30 m south of the outcrop similarly decreased from 40 individuals in 1973 (Graber and Brewer, 1985) to none in 1988. Overall, the small sub-populations seem prone to extirpation while the main population has remained viable for centuries.

In addition to native plants, there are currently several trans-

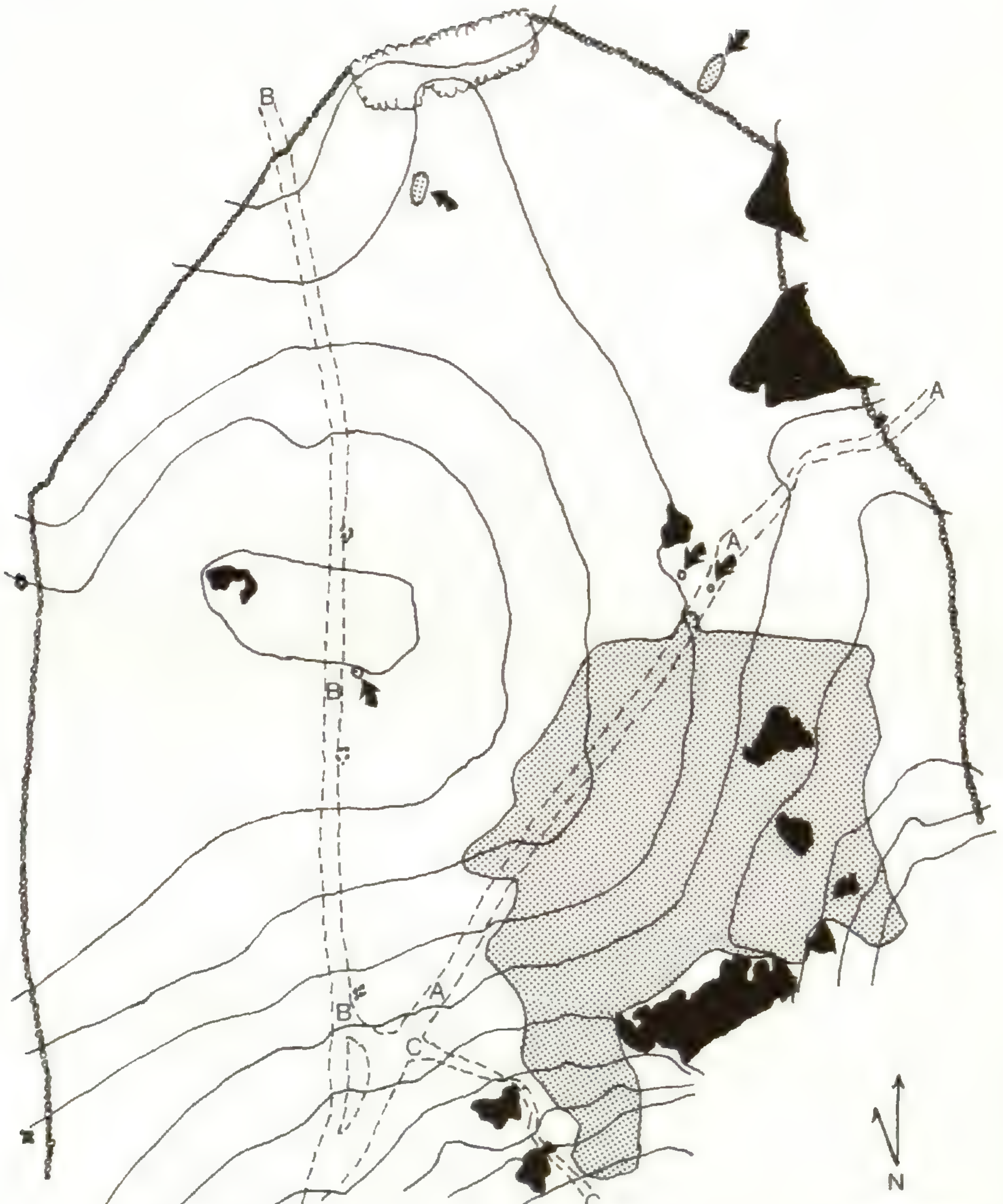


Figure 1. Map of Monroe Flats, Presidential Range, New Hampshire showing the current range of *Potentilla robbinsiana*. Shaded area is the extent of the main population of *P. robbinsiana* mapped in 1985; arrows indicate outlier sub-populations. One unmapped sub-population occurs 30 m south of the main population. Solid lines are contours in one-meter intervals below a datum at the high point of the knoll (ca. 1548 m). Dotted lines delimit the extent of the treadway

planted populations of *P. robbinsiana* established in the White Mountains. Three programs (i.e., Harris, 1964; Graber, 1974–85; AMC, 1986–89) have transplanted more than 500 individuals, grown from Monroe Flats stock, into at least six locations (i.e., Camel Patch, Oakes Gulf, top of Monroe Flats, Lakes Hut, Boott's Spur, North Lafayette).

Since the 1820's, *Potentilla robbinsiana* has been common on Monroe Flats. In August 1827, William Oakes observed "several hundred specimens" (ToCo, 8/1827). Considering its inconspicuous nature after flowering, Oakes' casual record is certainly a gross underestimate. Between 1824 and 1847, botanists removed more than 96 plants from the site, including at least 50 by Oakes himself. In several years at the turn of the century, hundreds of plants were collected at once. A minimum population of many hundreds must have been maintained as this heavy and sustained collecting occurred without comment or extirpation. In 1977, a casual estimate of the "population of ca. 300 plants" (NHA: *Crow #2449 & Hellquist*) was remarkably similar to that of 1827. Much of the population, however, was again overlooked as Graber (1980) had counted 1801 large plants in 1973. Some 1701 flowering plants were counted in 1992 (M. Iszard-Crowley, pers. comm.) and the population on Monroe Flats seems to have been relatively stable over the past 20 years (Graber and Brewer, 1985; Fitzgerald et al., 1990). For the last 165 years the population has certainly been in the hundreds, and probably had been in the thousands.

**Population on Franconia Ridge**

The first known Franconia *Potentilla robbinsiana* were near Mt. Lafayette. Tuckerman's 1840's collections were most likely from the accessible summit of "Great Haystack," the early name for Mt. Lafayette. On 10 July 1897 during an Appalachian Mountain Club (AMC) field meeting (Anon., 1898), Frederic Endicott collected a single *P. robbinsiana* from "near north summit of Mt. Lafayette" (GH). The third and last known collection was on 6

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of abandoned trails, specifically: A—the original Crawford Path (ca. 1840–1918); B—the Crawford Path (1915–83); and C—the Dry River Trail (ca. 1938–65). Large rocks and outcrops are solid. A scree wall built in 1983 to delimit the restricted area is shown as a chain.

July 1908 by an unknown "Hunt" on "Mt. Lafayette" (CONN). This collector was perhaps William S. Hunt, an amateur who collaborated with Endicott in producing a list of alpine plants collected on AMC trips (Fuller et al., 1907). The Mt. Lafayette station was apparently extant in 1908, but extirpated by 1915.

Since 1915, all *Potentilla robbinsiana* from Franconia have been found at a station well south of Mt. Lafayette. On 18 July 1915 during a weekend trip over Franconia Ridge, M. L. Fernald and his graduate student, F. J. Smiley, found *P. robbinsiana* on "damp gravel and crevices about the low north dome of Mt. Lincoln" (GH; FeCo, 8/1915). Fernald returned in August 1915 to scour the ridge, finding rare plants elsewhere, but *P. robbinsiana* was apparently restricted to the one site. On 13 June 1963, Fred Steele found *P. robbinsiana* still on Mt. Lincoln. Two plants, including one with 50 flowers which was the largest Steele had seen, were growing with dead moss "on sloping rock" or "sort of ledge" along the trail north of Mt. Lincoln (Steele, pers. comm.). Botanists, including Steele, saw three plants in July 1965 (Steele, personal herbarium notes), but were unable to locate any in the 1970's. On 24 June 1984, AMC hutman Rick Boyce, found two living *P. robbinsiana* when he "just happened to see a yellow flower" while hiking just south of Mt. Lincoln. The following year Charles Cogbill and Roger Collins found four additional flowering individuals in crevices on the cliff directly below these plants.

Sketchy records of *Potentilla robbinsiana* indicate several small historic populations scattered along Franconia Ridge. All Franconia reports total only 51 individuals. Their extremely limited numbers, spotty occurrence, and habitat on gravel, ledges, or cliffs, set them apart from those on Monroe Flats. Some 38 plants are known to have been collected from Franconia and 29 (57% of the plants ever known there) are from a single collection by M. L. Fernald (11725) in 1915. None has been collected since 1915. Only 13 separate flowering plants have been seen in thorough searches over the last 30 years (e.g., Steele, 1964; Crow, 1982; Cogbill, pers. obs.). The Franconia population was never large; its current (1991) population of five flowering individuals is imperiled at the known remaining station.

## Discounted Locations

Several herbarium collections from Mt. Washington sites are mislabeled. Tuckerman's 1839 herbarium labels (UPS, MASS, NEBC)

read: "Mt. Washington, N.E. [sic] side of the Peak." Despite incorrect dates and directions on the labels, his notes are explicit that he collected from Monroe Flats, "S.E. [sic] of the peak" (TuPa, 6/1839) and "not elsewhere" (UPS). Beaudry's collection from "Mt. Washington: 7-mile post" on 26 July 1958 (MT) was also mislabeled. His co-collectors that day did not find it there, actually collecting *P. robbinsiana* only from Monroe Flats (A. Löve, pers. comm.; Louis-Marie, QFA field notes). Two odd collections from "Tuckerman's Ravine" (NEBC: no collector and no date, but a H. G. Jesup 1890's label) and "Alpine Garden" (BSN: collector J. H. Emerton, 1907) have no other substantiation. Some herbarium sheets have indefinite locations such as "alpine region, New England," "White Mountains," or "Mt. Washington"; all except those from Franconia apparently are from the single Monroe Flats site.

No verifiable record of *Potentilla robbinsiana* exists outside New Hampshire. Speculation about a Vermont site is based on a specimen (NEBC) labeled "Mansfield Mt. E.T." found in 1979 among Robbins's material. Considering the notation, it has been interpreted as an Edward Tuckerman collection. Interestingly, Tuckerman's only known trips to Mount Mansfield, Vermont were in 1839 and 1840, and his field notes explicitly indicate that he did not find *Potentilla* then (TuPa, 7/1839; 7/1840). Apparently the label is not in Tuckerman's hand and was written after 1842 (Oakes, 1842). This enigmatic collection credited to Vermont (e.g, Crow, 1982; Gleason and Cronquist, 1991) remains dubious. Recent references (e.g., Countryman, 1980; Graber, 1980; Gleason and Cronquist, 1991) to an unvouchered sighting on a Vermont mountain from 1970 are based on a misidentification of *P. norvegica* from Mt. Equinox (Graber and Brewer, 1985).

## PERCEPTIONS AND REACTION TO RARITY

### Discovery Era: *Potentilla minima* 1824-60

Much of the early botanical exploration of the White Mountains was driven by the search for rare alpine species, including several found near Monroe Flats (Tuckerman, 1843; Bigelow, 1824; Oakes, 1847; Pickering, 1879; Pease, 1917, 1964). By the 1840's, Oakes considered a couple of local species "approaching exhaustion," presumably due to over-collection of rarities (Pease, 1917). Significantly, *Potentilla minima* never received the same attention

as these other species and was not even listed as "rare" (Spaulding, 1855). Lack of prominence of this species was exemplified by the fact that no one took credit for its discovery and by the failure of anyone, especially Nuttall or Oakes, to publicize or publish any description.

Early interest in *Potentilla robbinsiana* was driven by taxonomic considerations. Collectors were uncertain what taxon they found and were selectively exchanging specimens and intelligence (e.g., OaCoAAS, 4/1828; TuPa, 8/1839; TuCo, 12/1843). Even Tuckerman's early collections must have been limited as he was very concerned over the loss of some of his "rare" flowering *P. robbinsii* (sic) specimens (CuCo, 3/1840; 9/1840) and indicated that "my specimens are exhausted" (QK, 10/1840). Oakes' and Tuckerman's extensive and widely dispersed collections from Monroe Flats were fundamental in taxonomic work. Once Gray determined that it was part of a European alpine species (Torrey and Gray, 1840), it was no longer a "new" species and collections and interest diminished. Its well-known location, albeit obscure and disjunct from the Alps, rendered the White Mountain *P. minima* less of a rarity (TuCo, 12/1843; Tuckerman, 1860).

## Collection Era: *Potentilla frigida* 1860–1910

Following an increased public interest in natural history, vast botanical collections were made between 1860 and 1910 (Table 1). Completion of the carriage road to the summit of Mount Washington in 1861 gave convenient access to the long-known site at Monroe Flats. In June 1862, three collectors began an era of group collecting by taking 34 plants (17 sheets). During the collection peak of the Victorian era, botanists sought to document carefully the alpine flora by making regular collecting trips to Monroe Flats (Pease, 1917). For example, "in the last week of May [1878?]," Edwin Faxon climbed from Crawford Notch "to gather *Potentilla frigida* in flower in its alpine home, . . . the little plain by the ice-clad Lake of the Clouds" (Kennedy, 1900). Zealous botanists made mass collections on specific forays (e.g., 60 plants by 5 collectors on 5 June 1878; 59 plants on 15 August 1898; and 75 plants on 2 June 1903). In 1898 alone, 143 known individuals were collected. In all, some 73% of *P. robbinsiana* collections date from 1875 to 1909 with more than 403 individuals taken during just 9 years at the turn of the century. At its

maximum, collection pressure was significant, removing an equivalent of perhaps one-third of the present population in a decade.

In the late 1800's, botanists expressed little concern about *Potentilla frigida.* Monroe Flats continued to supply unrestricted collections as many sought rarities to expand their personal herbaria (e.g., Northrop and Northrop, 1910). The two most prolific collectors, Pringle in the 1870's and Eggleston in the 1890's, were even selling alpine plants, specifically including *P. robbinsiana,* to other collectors at 10 cents per sheet (Anon., 1878; EgPa, 1901). A few such as G. M. Allen (1888) recognized the "incursions of botanists," but he still "took but a tiny spray . . . [of *P. robbinsiana*] . . . and left the remainder of the plant."

The western edge of *Potentilla robbinsiana* habitat has historically been close to trails (Figure 1), in particular part of the original Crawford Path (ca. 1840–1918) and the Dry River Trail (ca. 1938–65). For over 150 years, collectors, horses, and hikers passed through the population on a cleared topographic treadway (Waterman and Waterman, 1989). Improvement of the Crawford "bridle" Path, trampling by its users, and easy access for collectors have arguably been the most significant human impact on the plants. Nevertheless, this trail section, abandoned in 1918, now supports a vigorous population of at least 71 flowering *P. robbinsiana.* Collecting and trail activities from 1840 to 1918 apparently did not permanently affect the population.

## Stewardship Era: *Potentilla robbinsiana* 1910-83

In 1915 Fernald made the last mass collection of *Potentilla robbinsiana,* nearly eliminating the population on Franconia Ridge. This was Fernald's only collection of this species, and reflected earlier unrestricted practice. Significantly, only 21 collections consisting of 56 specimens have been made at Monroe Flats since 1910 (Table 1). There were at least 15 individual collectors, but many explicitly showed restraint. For example, despite long-term interest in the plant, S. K. Harris collected only 3 plants for herbaria (1927–30) and F. Steele collected only 5 single plants (personal herbarium, 1934–56). In contrast, botanists associated with field excursions of the International Botanical Congress in Montreal in 1959, despite being asked not to collect it (Löve and Löve, mimeographed field guide, 1959), made at least six collec-

tions (19 plants). In the past 30 years, only three sheets of single plants have been collected, all by researchers working on the plant. Recently, plants have been used for chromosome counts (COLO: *Löve & Löve, 1962*), greenhouse cultivation (A. Löve, pers. comm.), transplants (Harris, field notes, 1964: 6 plants), vouchers (NHA: *Crow and Hellquist, 1977*), and "collected accidentally during a survey of the population" (MSC: *Brewer, 1983*).

In the mid-1900's, an emerging stewardship ethic spread among botanists and the hiking community. The very restricted distribution of *Potentilla robbinsiana* was documented and it was considered "probably the rarest plant to be found on the Presidential Range" (Harris, 1930, 1941). Botanists told their colleagues the plant is "scarce . . . please do not collect!" (Löve and Löve, mimeographed field guide, 1959), and asked the public to "please help protect this rare plant" (Bliss, 1963). Responding to increased curiosity about the plant, Harris and others in the 1960's showed visitors the small population west of the trail, rather than disturb the main population (C. Harris, pers. comm.). The Dry River Trail was even rerouted by those (i.e., S. K. Harris, W. N. Tiffney) who were concerned about its effect on erosion and several rare species (C. Harris, pers. comm.). Although recent human trampling has been considered a crucial impact (Graber, 1980; Graber and Crow, 1982; Graber and Brewer, 1985), effects associated with the post-1918 Crawford Path are minor in contrast to those in the past.

Due to efforts by interested botanists (e.g., F. Steele, R. Graber, G. Crow), the species was determined to be federally endangered. Following a recovery plan, Monroe Flats was closed to access in 1983 (Lanier and Hill, 1983). After nearly 75 years of informally decreasing human pressure, the species was legally protected from disturbance or collection. Recent human activities have been directed toward augmenting populations through trail relocation, access restriction, population monitoring and transplant programs (Fitzgerald et al., 1990). After 160 years of human influence, *Potentilla robbinsiana* is still tied to human intervention in the management era.

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## MANUSCRIPTS CITED

Citations to unpublished manuscripts are abbreviated:

CrPa—Crawford's register, 1823–35, Lucy Crawford Papers, MS 626 (3), Dartmouth College Special Collections

CuCo—letters: Tuckerman to Curtis 9/3/1840, 11/9/1840, Moses Ashley Curtis Papers, #199, Southern Historical Collection, University of North Carolina Library, Chapel Hill

EgPa—printed sheet [1901], Box 1, folder 10, W. W. Eggleston papers, MS–28, Dartmouth College Special Collections

FeCo—postcard: Smiley to Fernald, 15/8/1915, M. L. Fernald correspondence, Gray Herbarium

GrCo—letter: Gray to Hooker, 13/10/1839, A. Gray correspondence, Gray Herbarium

OaCoAAS—letters: Torrey to Oakes 24/4/1828, folder 18; and Tuckerman to Oakes 10/1844, folder 19; W. Oakes Correspondence, American Antiquarian Society
OaCoGH—extracts of letters: Oakes to Robbins 4/1829, 24/7/1829; and Oakes to Torrey 9/6/1834, folder 31; Biog 2 Oa 4, Box W, W. Oakes correspondence, Gray Herbarium
ToCo—letters: Oakes to Torrey: 3/8/1827, 3/4/1828, 15/4/1828, 3/4/1841; J. Torrey correspondence, New York Botanical Garden
TuCo—letters: Oakes to Tuckerman: 16/4/1841, vol. 3; 30/12/1843, vol. 5; Torrey to Tuckerman, 8/10/1840, vol. 3; E. Tuckerman, Jr. correspondence, American Antiquarian Society
TuPa—botanical journals, 1838–39, Box 1, folder 1a; 1840, Box 1, folder 1; Tuckerman Botanical Papers, Amherst College Archives

## HERBARIUM RECORDS CITED

Citation of herbarium acronym (Holmgren et al., 1990) indicates data or quotations from material contained on labels, annotations, or notes attached to herbarium sheets from that herbarium.

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# *SALIX VESTITA* PURSH AND *SAXIFRAGA OPPOSITIFOLIA* L.: ARCTIC-ALPINE SPECIES NEW TO NOVA SCOTIA

RENÉ J. BELLAND AND W. B. SCHOFIELD

During the course of bryological field work carried on for the Canadian Parks Service (Cape Breton Highlands National Park), we noted rare vascular plants but made no comprehensive collections. On the cliffs above Corney Brook, however, we discovered two arctic-alpine species not reported previously for the flora of Nova Scotia. *Salix vestita* Pursh and *Saxifraga oppositifolia* L. are here reported as new to the flora of the province:

Inverness County, Cape Breton Highlands National Park, Corney Brook gorge, 46°43′N, 59°53′W, 6 July, 1991. Elevation ca. 280 m.

Both species were extremely rare, each represented by a single plant. The single *Salix vestita* (*Belland, Schofield & Moniz de Sá 16587,* CAN) grew in a large, sheltered, deep crevice as a shrub ca. .75 m tall. The specimen was pistillate and appeared to be healthy; inflorescences were immature.

The single *Saxifraga oppositifolia* was present in an intermittent seep on a partly shaded rock face. The plant was small, lacked flowers or fruit, and appeared somewhat etiolated. Because of the scarcity of *S. oppositifolia* at the site, no vouchers were taken of this species. A clear photograph (CAN) was made and careful observations confirmed its identify. The distinctive "four-ranked opposite bristle-ciliate dorsally keeled . . . leaves" (Fernald, 1950) readily identify this species even when etiolated. We are convinced that other populations exist in the Cape Breton Highlands National Park, which await discovery through careful exploration of cliffs in upper reaches of watercourses.

The Corney Brook site is rich in arctic-alpine and boreal disjunct plants. On the same cliff we found *Achillea borealis* Bong., *Carex atratiformis* Britt., *C. capillaris* L. var. *major* Blytt., *C. scirpoidea* Michx., *Cystopteris fragilis* (L.) Bernh., *Draba arabisans* Michx., *Erigeron hyssopifolius* Michx., *Galium kamtschaticum* Steller, *Lycopodium selago* L., *Pinguicula vulgaris* L., *Primula mistassinica* Michx., *Saxifraga aizoides* L., *S. aizoon* Jarg.

var. *neogaea* Butters, *Scirpus caespitosus* L. var. *delicatulus* Fern., *Sedum rosea* (L.) Scop., *Senecio pauperculus* Michx., *Solidago multiradiata* Ait. and *Polystichum lonchitis* (L.) Roth. Among the bryophytes are *Cyrtomnium hymenophylloides* (Hueb.) Nyh. *ex.* Kop., *Entodon concinnus, Orthothecium strictum* Lor., *Plagiobryum zierii* (Hedw.) Lindb. and *Pohlia filiformis* (Dicks.) Andr.

These rare plants occurred on humid, north-facing cliffs. The site possesses many of the characteristics described by Hounsell and Smith (1968) for habitats in which arctic and boreal disjunct plants occur in Nova Scotia. The cliffs are sheltered in many places by tall trees. This effect, combined with the aspect, would create a cool microclimate throughout the growing season and one which would experience considerable snow accumulation during the winter.

Although many of the plants at the Corney Brook site are calcicoles, there is no evidence of calcareous rock (e.g., limestone, dolomite, basalt) at the site. In fact, many of the bryophyte species present grow only on noncalcareous rock (e.g., *Andreaea rupestris* Hedw., *Dicranodontium denudatum* (Brid.) Britt. *ex* Williams, *Diplophyllum taxifolium* (Wahlenb.) Dum., *Paraleucobryum longifolium* (Hedw.) Loeske).

The population of *Salix vestita* in Cape Breton represents its southernmost locality in eastern North America. The species is best represented in the Rocky Mountains, and occurs disjunct in the Hudson Bay area and in the Gulf of St. Lawrence region (Meusel et al., 1965) where it extends northward along the Labrador coast as far as 59°N (Nachvak). The Canadian Rocky Mountain distribution has been mapped recently by Brayshaw (1976) and Moss and Packer (1983). The world distribution is mapped by Meusel et al. (1965).

The station for *Saxifraga oppositifolia* also marks an unusual record; it is widely distributed elsewhere at calcareous sites in the Gulf of St. Lawrence region, occurring along the entire west coast of Newfoundland, and along the North Shore of Québec as far west as the Mingan Archipelago. The southernmost populations in eastern North America are in New England, on Mt. Mansfield, and the Willoughby Cliffs and Job Pond Cliffs, Vermont (Crow, 1982; Seymour, 1982) where it is local on the cliffs.

These two taxa, each represented by a single individual, represent very rare native species in the province; their protection by virtue of their location in the National Park is assured.

## ACKNOWLEDGMENTS

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# BOOK REVIEW

Stuckey, Ronald L. 1992. *Women Botanists of Ohio: Born before 1900.* 67 pp. Columbus, Ohio: Ohio State University, pb. Copies available from Ronald L. Stuckey, RLS Creations, P.O. Box 3010, Columbus, OH 43210. (Priced $11.50, includes mailing.)

Dr. Ronald L. Stuckey and the late Dr. Emmanuel D. Rudolph, botanists at Ohio State University, are interested both in botanical history and in the role of women in botanical science. Dr. Rudolph has written about the broader aspects of this subject; Dr. Stuckey is an expert on early mid-west botanical history and the part women have played. This collection of biographies was published for the May, 1992 meeting of The Council on Botanical and Horticultural Libraries held at Columbus, Ohio.

Librarians and historians of science, especially, appreciate such a gathering of scattered source material under one cover. Dr. Stuckey started to gather data on early Ohio botanists when he came to Ohio State in 1965. In 1973, he wrote a twenty-page biography and bibliography for the *Michigan Botanist* of Ohio's Dr. Emma Lucy Braun, one of our country's most eminent ecologists and botanists. The theme for the Ohio Academy of Science meeting in 1982 was "Women in Science." Dr. Stuckey presented a paper on fourteen women botanists born before 1900 who had made significant contributions. His continued research on this subject culminates in this book which is dedicated to the memory of two younger Ohio women botanists with distinguished teaching careers: Dr. Janice Carson Beatley (1919–87) and Dr. Jane Cynthia (McLoughlin) Decker (1935–88).

In the United States, before the beginning of the twentieth century, some 1454 women were active in various aspects of botany, according to Dr. Rudolph. Of fifty-five Ohio women in this list, Dr. Stuckey has selected eighteen for his book. His sketches include a picture, if available, biographical information, education, and mention of their most important publications and awards. Some of the women were professional botanists, some were amateurs, but all published papers and/or books on the results of their studies. Many were students of William Kellerman who came to Ohio State in 1891 (died 1908), and John H. Schaffner who was on the faculty from 1897 to 1931. Two of the women

married these professors. Stella Victoria (Dennis) Kellerman (1855–1936) assisted her husband with illustrations for his books, and in research. Independently she published her own research on the morphology of plants and flowers, notably on the tassel of the corn plant. Mabel (Brockett) Schaffner (1869–1906) assisted her husband and also did independent research. Her paper on the embryology of shepherd's purse (*Capsella bursa-pastoris*) is a classic.

The first woman botanist in Ohio was Eliza Griscom Wheeler (1817–50) who married William Sterling Sullivant, the distinguished bryologist, in 1834. She worked alongside her husband in the field, in the herbarium and in the office, and illustrated many of his books. By the mid- to late 1800's a number of women had become involved in collecting and in publishing local floras. The best known of this group was Harriet Louise Keeler (1844–1921), a teacher for forty years who wrote seven semi-popular books on northeastern native plants including *The Wild Flowers of Early Spring, Our Native Trees, Our Northern Shrubs,* and *The Wayside Flowers of Summer.*

Emily Katherine (Dooris) Sharp (1846–1935) often accompanied her doctor husband on his medical rounds by carriage in Madison County and developed a keen interest in collecting and studying plants and their habitats. She published her observations in a small book, *Summer in a Bog,* in 1913. Her chapter on the activities of earlier women botanists in Ohio was the only real source of such information until Dr. Stuckey's book. She added some 500 specimens to the herbarium under Dr. Kellerman's direction.

Dr. Clara Gertrude Weishaupt (1898–1991) was an outstanding teacher of general botany and local flora at Ohio State. She developed *The Vascular Plants of Ohio* (3rd ed., 1970), for her courses. She contributed the section on Gramineae in Braun's *Vascular Flora of Ohio, The Monocotyledonae,* Vol. 1. Concurrently with her teaching she was curator of the Ohio State University Herbarium, and was instrumental in reorganizing and revitalizing it after World War II.

Dr. Stuckey concludes his book with a six-page tribute to Dr. E. Lucy Braun, most famous for her pioneering studies in forest ecology and author of *Deciduous Forests of Eastern North America* (1950), *Woody Plants of Ohio* (1961) and *Vascular Flora of Ohio: The Monocotyledonae,* Vol. 1. There is an eleven-page bibliog-

raphy, a summary and additional statistics. Besides the botanical information in the book, Dr. Stuckey has included a set of the fourteen calendars which make up the Gregorian Calendar. These calendars, seven for even years and seven for odd years, are printed on the same pages as the portraits of the botanists. An explanation of the calendars is given in pages viii and ix of the Introduction. They are included because "TIME is the most important thing in your life." One might add that all eighteen of these women obviously made the very best use of time in their very full and accomplished lives.

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RHODORA, Vol. 95, No. 881, pp. 82–84, 1993

# BOOK REVIEW

Robert R. Ireland and Linda M. Ley. 1992. *Atlas of Ontario Mosses.* Syllogeus 70, Canadian Museum of Nature (v + 138 pp., including 490 maps and 2 figs.). Available from the Canadian Museum of Nature, Direct Mail Section, P.O. Box 3343, Station D., Ottawa, Ontario, Canada K1P 6P4. (No charge.)

Due to the efforts of Dr. Robert R. Ireland as curator of the bryophyte collections at the Canadian Museum of Nature, an enviable body of bryophyte data has been accumulated there. This atlas is another in a continuing series of publications of distributional data regarding the Canadian moss flora that has been accumulating for a long time. As Chairman of the Canadian Botanical Association Bryophyte Checklist Committee, Ireland organized, with other Canadian bryologists, a *Checklist of the Mosses of Canada* (Ireland et al., 1980), which effectively provided species lists for every province and territory in Canada. The checklist was revised seven years later (Ireland et al., 1987).

Ireland became familiar with the moss flora of western Canada while studying for his doctorate under Elva Lawton at the University of Washington, Seattle, making contributions to Lawton's *Mosses of the Pacific Northwest,* an important flora of the northwestern United States and adjacent Canada (Lawton, 1971). Upon becoming curator in the Bryology Section of the Canadian Museum of Nature at Ottawa, Ireland proceeded with taxonomic revisions in the Bryophyta, including treatment of neotropical bryophytes, and also concentrated on floristic research in the Maritime Provinces, Quebec and Ontario. In 1975, he, together with Ray F. Cain, produced a checklist of the mosses of Ontario detailed by political subunit (county, etc.) (Ireland and Cain, 1975), and in 1982, Ireland produced a major flora with keys, descriptions and illustrations of the moss flora of the Maritime Provinces (Ireland, 1982). In 1987, with Gilda Bellolio-Trucco, he wrote a useful, illustrated guide to many of the hornworts, liverworts, and mosses of eastern Canada for amateur botanists or professionals with little experience in the Bryophyta. Throughout the course of research activity, he has made skillful and generous use of the curatorial and herbarium assistants with whom he has collaborated.

With the *Atlas of Ontario Mosses,* written with Linda M. Ley, Ireland adds to the understanding of the Canadian flora by extending knowledge of the Ontario moss flora with 17 pages of phytogeographic discussion, two figures showing general physiographic and vegetational features, and 490 distribution maps of the known moss flora of that province. Textural topics include general essays on provincial physiography and geology, climate, vegetation, collectors, distribution patterns of Ontario mosses, and a short bibliography. What is new and valuable about this publication is that each species has its own dot map, showing, in many species, distinctive distributional patterns, and generally, greater biodiversity in the south, reflecting the situation with vascular plants. Such patterns are not much discussed, however, other than assignment to the categories "Widespread, Southern, Northern, Eastern, and Western," which are not referred to other phytogeographic studies. For instance, although the Niagara Escarpment is mentioned in the discussion of geology as "a northeasterly facing cuesta of Silurian carbonates" extending from Niagara Falls through the Bruce Peninsula and Manitoulin Island, there is no mention of the common and distinctive correlation of this important Ontario feature with the distributions of calciphilic species. Perhaps Ireland plans more detailed discussion of geographic patterns of Ontario mosses in a future work.

The species maps include river systems as details but no political, physiographic or vegetational subunits. There are no overlays provided; one can try to mentally overlay the political map included with the 1975 Ontario checklist or leaf back and forth to the physiographic and vegetational maps in Figures 1 and 2. For some readers, however, this lacks exactitude, which is especially unfortunate in that considerable collecting since the 1975 checklist is reflected in the Atlas, and additions to counties and other subprovincial political areas are very difficult to locate and assign. The maps are of little value to local workers interested in local floras. Thus, the Atlas cannot be considered an "extension" to the 1975 checklist in the sense of being an update, but is something else entirely.

The maps have value in showing the relative success of particular species in the various temperate and boreal zones of Ontario, and will be valuable in helping to determine range limits for species in the Bryophyte volume of the ongoing Flora North America project. Thus, although the major criticism of this work

is that Ireland and Ley missed an opportunity to interpret the actually quite interesting distributional patterns of the Ontario moss flora, this work is valuable in its contribution to the understanding of moss distributional patterns, which are often surprisingly wide and curiously different in many ways from those of vascular plants at the same taxonomic level. We look forward to additional contributions from Dr. Ireland and the Bryology Section at the Canadian Museum of Nature.

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**Cover Illustration**

*Amelanchier nantucketensis* Bickn., the Nantucket Shadbush, is found only on dry moors, pine-barrens and pond margins on Nantucket and Martha's Vineyard Islands. A surculose, loosely colonial shrub to 2 m, this member of the Rosaceae is currently a candidate plant for federal listing. Original artwork by Alison Dibble.


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# THE HYBRID ORIGIN OF *ELEOCHARIS MACOUNII*

PAUL M. CATLING AND STUART G. HAY

## ABSTRACT

For nearly a century since its description, *Eleocharis macounii* Fernald has been known with certainty only from the type station in Québec. It has been treated as a synonym of either *Eleocharis intermedia* Schultes, *E. obtusa* (Willd.) Schultes, *E. ovata* (Roth) R. & S. or *E. palustris* (L.) R. & S., or as a hybrid. Various quantitative and qualitative morphological features suggest that it is a hybrid involving *E. intermedia* in series *Palustriformes* and *E. obtusa* in series *Ovatae*. *Eleocharis* × *macounii* is best distinguished from sympatric species by its rhizome internodes less than 2 mm long, presence of many culms of varying lengths arising from a single tuft and pale greenish-brown achenes with prominent keels and a rough cellular surface. This natural hybrid is of particular interest since it is the first reported in the genus *Eleocharis* in North America, and it involves different species groups within the genus.

Key Words: *Eleocharis* × *macounii*, Cyperaceae, hybrid, Québec, North America

## INTRODUCTION

The genus *Eleocharis* (Cyperaceae), commonly known as the spikerushes, is receiving increasing attention in North America because of the potential use of several species in aquatic weed management in irrigation systems and in pollution abatement (e.g., Sutton, 1984). The classification and identification of many of the species remain problematic. One of the problems is the status of *Eleocharis macounii* Fernald, a plant described in 1899 from specimens collected by J. Macoun at North Wakefield, Québec.

Marie-Victorin (1935) treated *Eleocharis* × *macounii* as a species, noting that it was known only from the Gatineau River. Svenson (1937) also treated it as a species but suggested that it



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was problematic, close to *E. intermedia* Schultes, and also had characteristics of the European *E. multicaulis* (Sm.) Desv. It was treated as a species in the 7th and 8th editions of Gray's Manual (Robinson and Fernald, 1908; Fernald, 1950). Fernald noted that *E. macounii* was similar to the North American *E. intermedia* Schultes and the European *E. carniolica* Koch. Later Svenson (1953) noted that *E. macounii* was best treated as "an estuarine modification of *E. obtusa* (Willd.) Schultes, and he treated it as a synonym of *E. obtusa* in his (1957) monograph suggesting that it was "a variant with elongated style base somewhere between *E. obtusa* and *E. ovata* (Roth) R. & S., in which some of the achenes are slightly trigonous." Svenson (*in* Kartesz and Kartesz, 1980) placed *E. macounii* in synonymy with *E. obtusa* var. *obtusa.* However, Hines (1975) in his monograph of the *E. ovata* complex (which includes *E. obtusa*) did not mention *E. macounii* under either *E. obtusa* or *E. ovata.*

Gleason and Cronquist (1965) placed *Eleocharis macounii* in synonymy with *E. intermedia,* and it is treated in the same way in the United States national list of scientific plant names (Anon., 1982).

With respect to Canadian literature, *Eleocharis macounii* was treated as a questionable synonym of *E. intermedia* by Scoggan (1978), omitted by Boivin (1967), and is not mentioned in the listing of the rare plants of Québec (Bouchard et al., 1983). In his recently published Cyperaceae of eastern Canada, Boivin (1992) placed *E. macounii* in synonymy with *E. ovata sensu lato* (i.e., including *E. obtusa*).

The only annotation on the type at GH is that of Boivin (dated 1979) which indicates his view that the material is referable to *E. palustris* (L.) R. & S. *sensu lato,* but with the rhizomes, a distinctive feature of the latter species, broken off. On the isotype sheet at CAN, S. G. Hay noted in 1988 that *E. macounii* is probably a partly sterile hybrid between *E. intermedia* and *E. obtusa* var. *jejuna* Fernald. Hay also uncovered another specimen of *E. macounii,* misidentified as *E. intermedia,* collected from Cascades (*Malte* 7.8.1913, CAN), a locality situated close to the type station.

In summation *Eleocharis macounii* has been regarded as a species, as part of the variation within one of four other taxa, or as a hybrid. The purpose of the present paper is to examine critically each of these possibilities, and particularly to consider the hypothesis that *E. macounii* is of hybrid origin.

## METHODS

The percentage of fruit development was determined on 15 mature spikes from the type material of *Eleocharis macounii* at GH and CAN. Pollen from five different spikes, also from the type material, was stained using the phloxine and fast green technique (Owczarzak, 1952) to assess fertility.

In order to determine whether *E. macounii* was intermediate in quantitative characters, 10 characters (Table 1) were measured in thirty specimens of each of *E. intermedia, E. obtusa* and *E. ovata.* These were selected to represent variation over a broad area of eastern Canada. For *E. macounii* two culms from the right hand group of tufts and two from the left hand group on the holotype were measured. Sheath length (mm) was measured from the base of the culm to the top of the sheath. Sheath width was measured across the mouth. Culm width was measured 1 cm below the inflorescence. Culm height is the distance from the tip of the spike to the base of the culm. Scales (also frequently referred to as bracts) measured were in all cases taken from the middle of the inflorescence. The length of the scarious margin of the scale was measured from the apical margin back to where it was no longer translucent. The length of the achene was measured from the base of the basal portion below the bristles to the base of the tubercle.

Tubercle width was used to separate *E. ovata* and *E. obtusa* since it is more easily determined than stamen number and separates the species readily (Hines, 1975). Here plants with a tubercle less than .5 mm wide are treated as *E. ovata,* while plants with a tubercle more than .51 mm wide are treated as *E. obtusa.*

## RESULTS AND DISCUSSION

Fernald (1899) noted with his original description of *Eleocharis macounii* that it resembled the European *E. carniolica* Koch in habit and inflorescence. He correctly noted, however, that *E. macounii* has a much broader tubercle (Figure 1B) than *E. carniolica.* Furthermore the surface of the achene of *E. carniolica* is not clearly cellular, but rather obscurely wrinkled longitudinally and the tubercle of *E. carniolica* has a much more distinct neck.

The European *Eleocharis multicaulis* (Sm.) Desv. is similar to *E. macounii* in some respects, but is a much more robust plant

Table 1. Minimum, maximum and mean values for 14 characters in four northeastern North American *Eleocharis* taxa. For *E. intermedia*, *E. obtusa* and *E. ovata*, $n = 30$. For *E.* × *macounii* $n = 4$, but see also accompanying description based on all available material. All measurements are in mm.

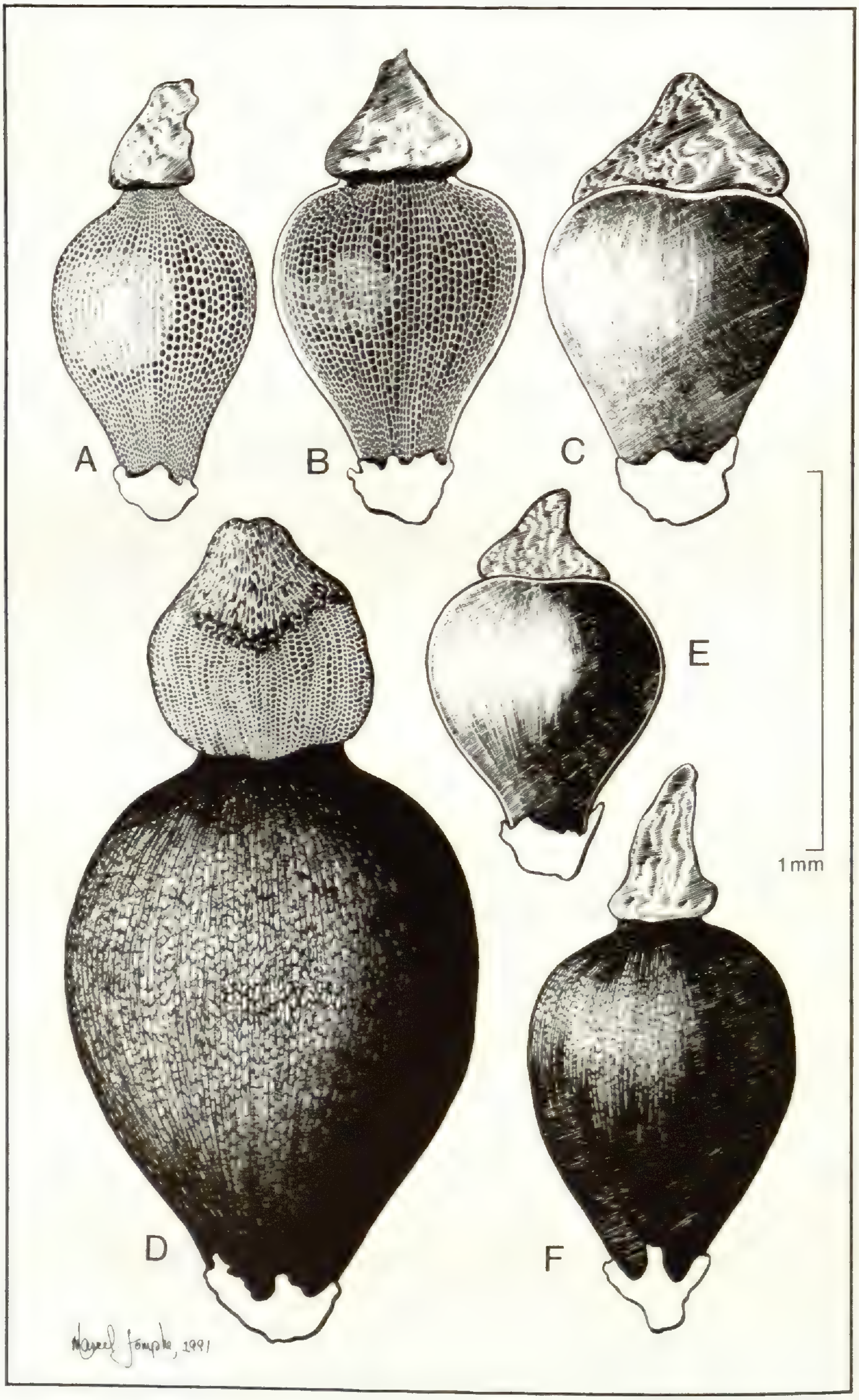
| | *E. intermedia* | | | *E. ovata* | | | *E. obtusa* | | | *E.* × *macounii* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Character | Min. | Max. | Mean | Min. | Max. | Mean | Min. | Max. | Mean | Min. | Max. | Mean |
| Sheath length | 7.00 | 20.00 | 13.80 | 14.00 | 37.00 | 22.13 | 21.00 | 60.00 | 34.53 | 18.00 | 27.00 | 21.75 |
| Sheath width | 0.42 | 0.78 | 0.53 | 0.58 | 1.16 | 0.84 | 0.78 | 1.56 | 1.10 | 0.64 | 0.88 | 0.73 |
| Culm width | 0.30 | 0.40 | 0.34 | 0.36 | 0.82 | 0.56 | 0.56 | 1.24 | 0.77 | 0.50 | 0.74 | 0.58 |
| Culm height | 50.00 | 187.00 | 120.00 | 49.00 | 286.00 | 159.47 | 132.00 | 455.00 | 220.00 | 95.00 | 168.00 | 139.25 |
| Spike length | 3.90 | 7.00 | 5.05 | 4.00 | 9.00 | 5.81 | 4.50 | 11.50 | 7.26 | 8.50 | 11.50 | 10.15 |
| Spike width | 1.90 | 2.80 | 2.30 | 2.60 | 4.00 | 3.27 | 2.90 | 4.00 | 3.53 | 2.40 | 2.80 | 2.55 |
| Scale length | 1.70 | 2.10 | 1.91 | 1.70 | 2.20 | 1.89 | 1.74 | 2.30 | 1.96 | 2.26 | 2.36 | 2.30 |
| Scale width | 0.94 | 1.28 | 1.09 | 0.90 | 1.20 | 1.03 | 1.00 | 1.40 | 1.15 | 1.08 | 1.28 | 1.14 |
| Scale width 0.2 mm from apex | 0.16 | 0.40 | 0.22 | 0.40 | 0.70 | 0.54 | 0.46 | 0.72 | 0.61 | 0.48 | 0.68 | 0.57 |
| Scale scarious apical margin width | 0.02 | 0.12 | 0.07 | 0.10 | 0.24 | 0.18 | 0.12 | 0.24 | 0.20 | 0.16 | 0.18 | 0.17 |
| Achene length | 0.98 | 1.12 | 1.03 | 0.80 | 0.96 | 0.86 | 0.90 | 1.04 | 0.99 | 1.00 | 1.10 | 1.05 |
| Achene width | 0.60 | 0.70 | 0.64 | 0.60 | 0.76 | 0.68 | 0.70 | 0.86 | 0.79 | 0.68 | 0.76 | 0.72 |
| Tubercle height | 0.26 | 0.44 | 0.35 | 0.26 | 0.38 | 0.31 | 0.26 | 0.42 | 0.33 | 0.40 | 0.42 | 0.41 |
| Tubercle width | 0.18 | 0.22 | 0.20 | 0.32 | 0.44 | 0.37 | 0.54 | 0.74 | 0.63 | 0.38 | 0.43 | 0.41 |

with much longer scales and broader spikes. It also has a slightly longitudinally wrinkled achene surface unlike *E. macounii*. Thus *E. macounii* is not a European introduction.

Boivin suggested on his annotation label that the type material of *Eleocharis macounii* is referable to *E. palustris* with rhizomes broken off. This suggestion has to be rejected for several reasons: the cellular achene surface (Figure 1B), the presence of culms of varying lengths from very short to very long (Figure 2A), the fact of many culms arising from the same point on an abbreviated rhizome (Figure 2A), the elliptic scales (Figure 2C), the relatively broad tubercle (Figure 1B) and the relatively pale greenish-brown mature fruit are all characters lacking in *E. palustris sensu lato* (Figures 1D, F, 2E, H), including *E. erythropoda* Steudel (*E. calva*, and *E. smallii* Britton).

The type material of *E. macounii* does not represent a freak, because the plants do not show any abnormal growth or infection. Only 10–30% of the flowers on spikes of *E. macounii* have well developed fruit, the remainder being aborted. Many *Eleocharis* species including *E. intermedia*, *E. ovata*, and *E. obtusa* invariably have 95–100% of the flowers ripening into achenes, in the absence of obvious fungus infection or insect attack. The high level of fruit abortion in *E. macounii* suggests that it may be a hybrid. The hybrid concept is further supported by pollen infertility since only 10% of the pollen from one spike and 40% of the pollen from another spike, both from the holotype of *E. macounii*, took up the stain. In contrast more than 90% of pollen grains from *E. intermedia*, *E. ovata*, and *E. obtusa* stained well. Even in the *E. macounii* pollen that did stain, the stain was often pale or confined to a small part of the grain.

The cellular, three-sided and greenish surface of the achenes on the holotype plants of *Eleocharis macounii* (Figure 1B) is suggestive of *E. intermedia* (Figure 1A), although these characters are less pronounced than in the latter species. If *E. intermedia* is one parent, as evidenced by the cellular achene surface, then the other parent may be expected to possess certain features expressed in *E. macounii*, but not in *E. intermedia*. Among these characters that are to be expected is a broad tubercle (Figure 1B), a keeled and lenticular achene, a relatively long spike, and blunt, broad-tipped scales that have a relatively broad hyaline margin apically. There are two possibilities in the general region: *E. obtusa* (Figures 1C, 2D) and *E. ovata* (Figures 1E, 2G). *Eleocharis erythropoda*


A
B
C
D
E
F
1 mm
Hazel Temple, 1991

(previously widely known as *E. calva*) and the *E. smallii-palustris* complex are eliminated as a source of putative parents because a hybrid of either of them with *E. intermedia* would be expected to have more pointed and broad-based scales and an achene with an elongate and fleshy tubercle and lacking prominently keeled edges, and rhizomes developed to a greater or lesser extent. *Eleocharis macounii* on the other hand has broadly rounded scales (Figure 2C), achenes with a relatively short tubercle and two or three prominently keeled edges (Figure 1B), and lacks an elongated rhizome. *Eleocharis obtusa* and *E. ovata,* however, both possess many of the characters to be expected in the other parent, notably the prominent keels on the achene, especially just below the tubercle. Both *E. obtusa* and *E. ovata* possessed values for various quantitative characters, such as tubercle width (Figure 1B) that were similar to *E. macounii* or intermediate with respect to *E. intermedia.* With regard to these two species, *E. ovata* has relatively short spikes and scales, and smaller achenes (Table 1), whereas relatively longer spikes and scales and larger achenes are predicted in the other parent if *E. macounii* were to be intermediate in these characters (Table 1). Since intermediacy is likely in many features of hybrids, *E. obtusa* is a more likely parent. It seems undesirable to recognize the var. *jejuna* of the latter species (e.g., Hines, 1975). The local rarity of *E. ovata* (Di Labio and Brunton, 1989; see also *M. O. Malte,* 4 Sept. 1922, *sub E. intermedia,* CAN) and the fact that it has not been found at Wakefield, where *E. obtusa* is common, also suggests that the latter is more likely to be the other parent.

*Eleocharis* ×*macounii* appears to be the first hybrid reported in the genus *Eleocharis* in North America, and it should at least raise the question of whether hybridization is more widespread in the genus than currently recognized, and associated with some of the taxonomic difficulties.

Natural hybrids in *Eleocharis* have been reported from Japan (e.g., Koyama, 1961), and hybrids in *Eleocharis* subseries *Palustres* in Europe have been well documented (Strandhede, 1965)

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Figure 1. Representative fruits of A *Eleocharis intermedia* (*Catling* 7/09/87, DAO). B *E.* ×*macounii* (*Macoun 7552,* GH). C *E. obtusa* (*Cody 6579,* DAO). D *E. palustris* (*Gillet 11765,* DAO). E *E. ovata* (*Dore 24360,* DAO). F *E. erythropoda* (*Rolland-Germain 10284,* DAO). Drawings by Marcel Jomphe.

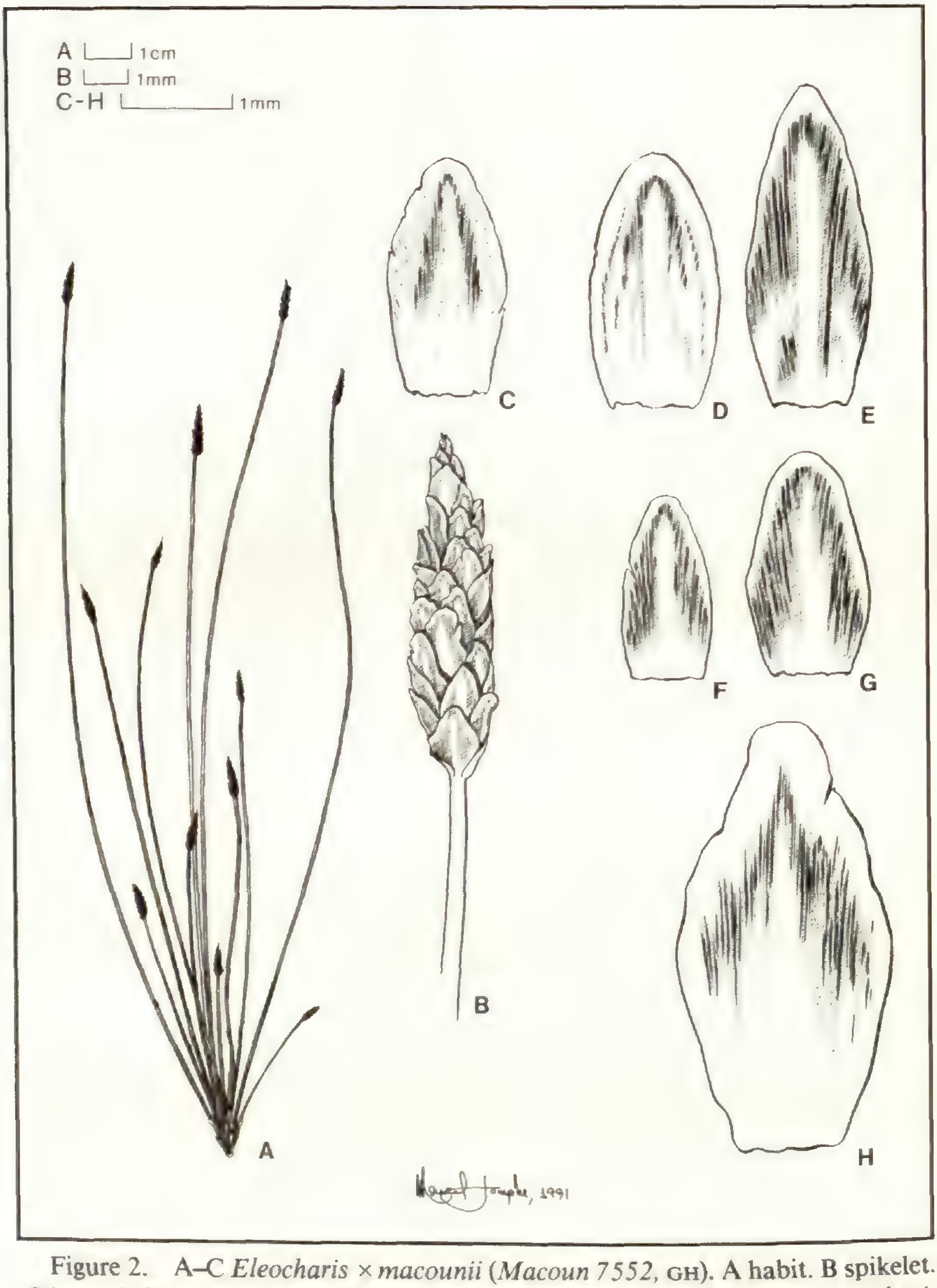


Figure 2. A–C *Eleocharis* × *macounii* (*Macoun 7552*, GH). A habit. B spikelet. C lower inflorescence scale. D–H lower inflorescence scales of various *Eleocharis* species. D *E. obtusa* (*Cody 6759*, DAO). E *E. erythropoda* (*Rolland-Germain 10284*, DAO). F *E. intermedia* (*Catling* 7/09/87, DAO). G *E. ovata* (*Dore 24360*, DAO). H *E. smallii* (*sub E. palustris* var. *major*, *Gillet 11765*, DAO). Drawings by Marcel Jomphe.

with cytological studies. *Eleocharis mamillata* subsp. *mamillata* × *E. palustris* subsp. *palustris* has greatly reduced fertility. It is to be expected that a hybrid between quite different species in different series (as treated by Svenson, 1957), like *E.* ×*macounii,* would also have reduced fertility. The chromosome number of *E. obtusa* is 2n=10, whereas *E. intermedia* has been reported with 2n=22 (Schuyler, 1977), so that if living plants of *E.* ×*macounii* are discovered, it should be possible to support the putative parentage with both chromosome number and meiotic anomalies. Unfortunately repeated attempts by the authors and other botanists to locate living material of *E.* ×*macounii* at the type station and elsewhere have been unsuccessful.

The following key and description, based on the type material and one other collection, will facilitate the identification of *E.* × *macounii.*

## KEY TO THE *ELEOCHARIS* SPECIES OF SOUTHERN ONTARIO AND QUÉBEC WITH DIFFERENTIATED TUBERCLES, FIRM SHEATHS AND ACHENES LACKING LONGITUDINAL RIDGES

1. Rhizome internodes more than 2 mm long, tufts with most culms of similar height ..... 2
   2. Achenes with a roughened cellular or reticulate surface, 3-sided .....
      .. perennials of series *Palustriformes* subseries *Truncatae* including *E. compressa, E. elliptica* and *E. nitida*
   2. Achenes essentially smooth and shiny, at most only obscurely cellular or reticulate, 2-sided .....
      .. perennials of series *Palustriformes* subseries *Palustris* including *E. erythropoda* and *E. smallii*
1. Rhizome internodes less than 2 mm long, tufts with culms of many different ages and heights ..... 3
   3. Achenes with a roughened cellular or reticulate surface 4
      4. Longer spikelets 5–7 mm long; achenes becoming dark green, without prominent keels, subterete to equilateral triangular in cross section; tubercles 0.18–0.22 mm wide ..... *E. intermedia*
      4. Longer spikelets 8–11 mm long; achenes pale greenish-brown, with 2 or 3 keels very prominent below tu-

bercle, more or less lenticular in cross section; tubercles (0.2)0.3–0.5 mm wide ..... *E.* ×*macounii*

3. Achenes with a smooth surface ..... 5
   5. Tubercle less than 0.5 mm wide ..... *E. ovata*
   5. Tubercle 0.51 mm or more wide ..... *E. obtusa*

**Eleocharis** ×**macounii** Fernald (*pro sp.*) (*E. intermedia* Schultes × *E. obtusa* (Willd.) Schultes), Proc. Amer. Acad. 34: 497, Figure 26a. 1899.

TYPE: Québec, North Wakefield, 13 Sept. 1893, *J. Macoun 75.5.2* (HOLOTYPE—GH! ISOTYPE—CAN!).

Annual herb; rhizome internodes less than 2 mm long, culms red at the base, green above, erect to divergent or bending downward, numerous, 20–230 mm long and of greatly varying lengths within a tuft, 0.3–0.8 mm wide 1 cm below the inflorescence; uppermost sheaths 5–35 mm long, 0.3–0.9 mm wide at the acute apex. Spikelets lanceolate, acute, densely 5–52-flowered, 3–11 mm long, 1.5–3 mm wide; scales reddish-brown with green midrib, ovate, obtuse, those in the middle of the spikelet 1.8–2.5 mm long, 1–1.3 mm wide, with a scarious margin 0.1–0.2 mm wide at the apex. Stamens 3, filaments 0.9–2 mm long, anthers 0.2–0.4 mm long, not reaching to the top of and concealed by the subtending scale, pollen largely infertile. Styles mostly trifid, occasionally bifid, the branches 0.5–0.9 mm long, extending beyond the tip of the subtending scale. Achenes mostly aborted, those maturing pale greenish-brown when fully mature, obovoid, 0.9–1.1 mm long (excluding tubercle), 0.6–0.8 mm wide, with mostly 3 (sometimes 2) keels becoming very prominent toward the apex, the surface rough-cellular, i.e., with circular or rectangular depressions with elevated walls; tubercle deltoid 0.3–0.4 mm high, 0.2–0.5 mm wide; bristles (4)5–6(7), brown, retrosely barbed, mostly 1.2–2.1 mm long, much exceeding the achene and tubercle.

*Additional material examined:* **Québec:** Cascades, 7-8-1913, *M. O. Malte s.n.* (CAN).

*Distribution:* Collected only from Wakefield and Cascades, both localities along the Gatineau River of Québec.

*Comments: Eleocharis* ×*macounii* lacks elongate rhizomes and has the tufted or caespitose growth habit of *E. obtusa* and *E. intermedia,* as well as flowering/fruiting culms of many lengths as in these species. This latter feature, as well as the more or less

diverging culms, readily distinguishes it from *E. erythropoda,* which it otherwise resembles.

There is reason to suspect that *Eleocharis* ×*macounii* may have culms longer than 230 mm and more than 1 mm wide, with larger spikelets than noted above, based on broken culms on tufts on both the holotype and isotype sheets, but these tufts cannot be identified with certainty. The material collected by *Malte* more closely resembles *E. intermedia* by its shorter culms and achenes with narrower tubercles.

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# THE MARINE AND BRACKISH WATER SPECIES OF *VAUCHERIA* (TRIBOPHYCEAE, CHRYSOPHYTA) FROM CONNECTICUT

CRAIG W. SCHNEIDER, LAURA A. MACDONALD, JAMES F. CAHILL, JR.,[1] AND SARAH W. HEMINWAY

## ABSTRACT

A more than decade-long field investigation of the genus *Vaucheria* in Connecticut salt marshes and estuarine habitats has revealed the presence of nine species, including five species and a variety not previously known for the area: *V. arcassonensis, V. compacta* var. *koksoakensis, V. coronata, V. intermedia, V. minuta,* and *V. nasuta.* Culture conditions in the laboratory stimulated production of gametangia, allowing for identification of mostly vegetative field-collected samples in their native muds. All marine and brackish water species of *Vaucheria* previously reported from other parts of New England are now known from Long Island Sound.

Key Words: *Vaucheria,* Vaucheriaceae, Tribophyceae, Long Island Sound, Connecticut

## INTRODUCTION

In his comprehensive flora of the green algae of North America, F. S. Collins (1909) included the then poorly known family Vaucheriaceae, listing just three marine species of *Vaucheria* from New England. Since that time, a number of studies has greatly increased our understanding of the family, culminating in the publication of a seminal monograph on the North American Vaucheriaceae by J. L. Blum (1972). This work prompted regional marine studies of *Vaucheria* in localities on the continent where the genus was poorly known, including Ott and Hommersand (1974) in North Carolina, Bird et al. (1976) in Nova Scotia, Pecora (1976, 1977, 1978, 1980) in Louisiana and Texas, Gallagher and Humm (1981) on the Florida Gulf coast and Garbary and Fitch (1984) in British Columbia and Washington. However, areas remain in North America, including much of New England, where the genus has not been investigated systematically. When compiling the list of seaweeds for Connecticut (Schneider et al., 1979), the first author recognized the paucity of species records in the

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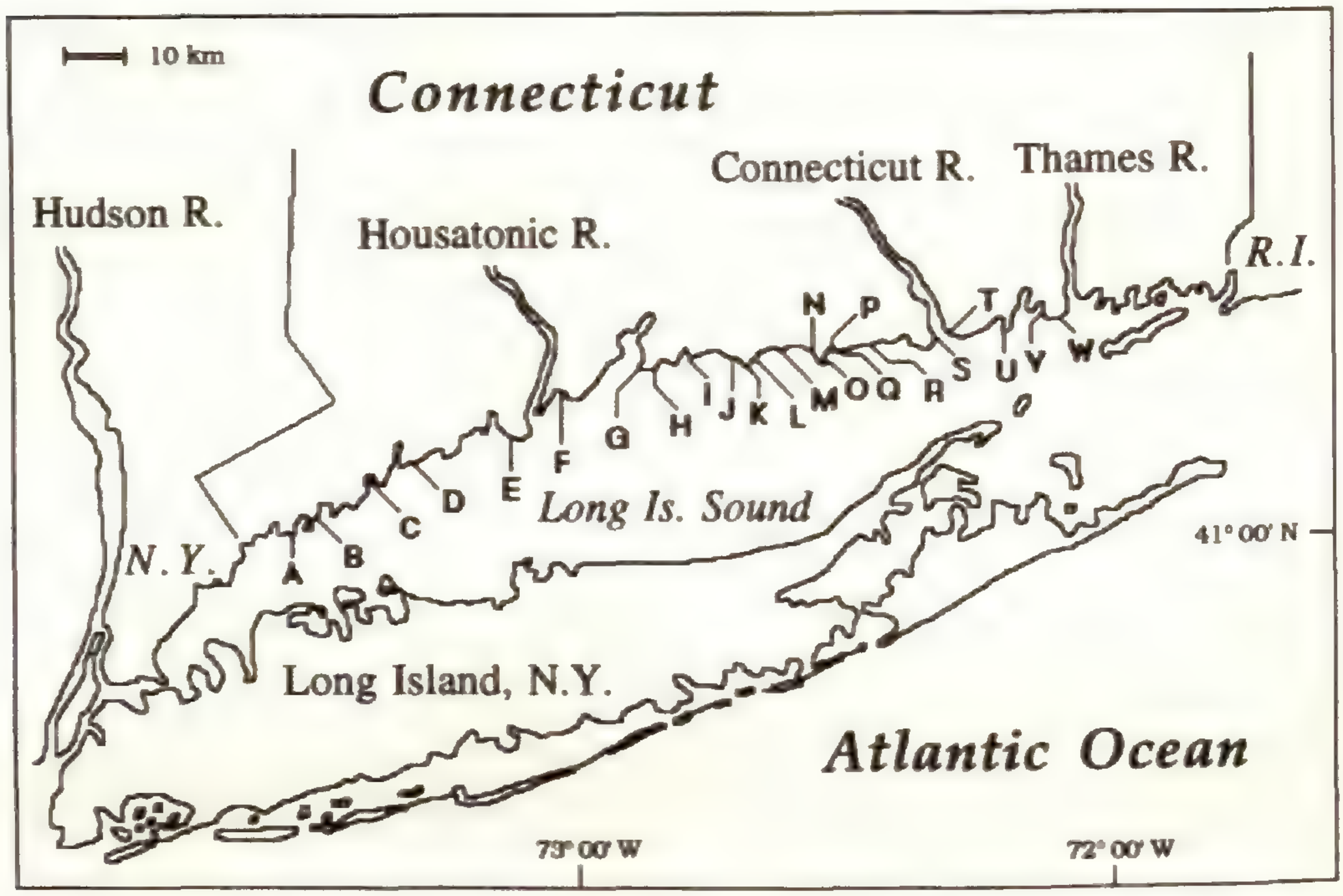


Figure 1. Map of the study area. For specific collecting site codes, see Table 1.

state relative to other areas in New England, in particular Massachusetts, and initiated the study reported here. At the time, only four marine species of *Vaucheria* had been reported from Connecticut: *V. compacta* (Collins) Collins ex W. R. Taylor (as *V. piloboloides*), *V. litorea* C. Agardh, *V. velutina* C. Agardh (as *V. thuretii*, Collins, 1900), and *V. vipera* Blum (Collins, 1900; Blum, 1972).

In part, the relatively small number of species known at that time for Connecticut, a state with a 160 km coastline divided by dozens of rivers and streams entering Long Island Sound, reflected the few collections made in the area. Furthermore, most collections were taken in the drier summer season, not during the autumn-winter-spring period of optimal growth and reproductive conditions for most *Vaucheria* species (Blum and Conover, 1953; Blum, 1966). Although *Vaucheria* is a common constituent of salt marsh and estuarine muds, it is most often found in the vegetative state, thereby proving impossible to distinguish at the species level. Previous workers (e.g., Ott and Hommersand, 1974; Pecora, 1976) found that suitable laboratory culture conditions would first allow luxuriant vegetative growth from the mud platform and then gametangial production, giving a more complete floristic assessment of *Vaucheria* species within a habitat.

Table 1. Long Island Sound collection sites.

| | |
|---|---|
| A | Fairfield Co., Greenwich Point Park salt marsh, Greenwich (GPP) |
| B | Fairfield Co., Cove Island Park salt marsh, Stamford (CIP) |
| C | Fairfield Co., mouth of Silvermine River, east bank, East Norwalk (SLV) |
| D | Fairfield Co., Sherwood Island State Park salt marsh, Westport (SHI) |
| E | Fairfield Co., Pride's Point, tidal channel vic. Housatonic River, Stratford (PPS) |
| F | New Haven Co., Milford Point salt marsh, Milford Harbor, Milford (MLH) |
| G | New Haven Co., Morris Creek salt marsh, Lighthouse Point, East Haven (MOR) |
| H | New Haven Co., Mansfield Point salt marsh, East Haven (MNS) |
| I | New Haven Co., Indian Neck Inlet salt marsh, Branford (INI) |
| J | New Haven Co., Island Bay salt marsh, Leetes Island, Guilford (LTS) |
| K | New Haven Co., Joshua Cove salt marsh, Sachem Head, Guilford (JCV) |
| L | New Haven Co., Chaffinch salt marsh, Guilford Harbor (CGH) |
| M | New Haven Co., Seaview Beach salt marsh, Madison (SVM) |
| N | New Haven Co., Hammonasett State Park salt marsh, Madison (HSP) |
| O | Middlesex Co., Meig's Point salt marsh, mouth of Hammonasett River, Clinton (HRC) |
| P | Middlesex Co., mouth of Indian River, east bank, Clinton (IRC) |
| Q | Middlesex Co., Clinton Beach salt marsh, Clinton (CBC) |
| R | Middlesex Co., Menunketesuck River, river banks, Grove Beach (GRV) |
| S | New London Co., Saybrook Point salt marsh, Old Saybrook (OSP) |
| T | New London Co., Blackhall River, river banks, Old Lyme (BOL) |
| U | New London Co., Rocky Neck State Park salt marsh, East Lyme (RNS) |
| V | New London Co., Pleasure Beach salt marsh, Waterford (PBW) |
| W | New London Co., Harkness Memorial State Park salt marsh, Waterford (HMW) |

## MATERIALS AND METHODS

Since the initiation of this study in 1980, we have visited more than 20 salt marsh and estuarine habitats along the Connecticut coast of Long Island Sound from Greenwich to New London (Figure 1), often revisiting the same sites in different seasons as well as years. The distance to collecting sites from Hartford accounted for the unevenness in visits to different sites. For example, we have taken nearly a hundred samples from over 20 visits to Harkness Memorial State Park, the most frequently visited salt marsh, but only visited the most distant locality, Greenwich Point Park, once. Few collections were made during summer, a period when typically high temperatures, high light intensities and lower rates of precipitation do not foster obvious growth of *Vaucheria* in Long Island Sound salt marshes.

Codes identifying the collecting sites are given in Table 1. At each collecting site in close proximity to a tidal channel or stand-

ing water, quadrats of mud 42.25 $cm^2$ and 2–3 cm thick (size compatible with culture vessels) with visible *Vaucheria* siphonous filaments or mats, were cut with a serrated knife and removed with a broad spatula. Mud samples without obvious *Vaucheria* were taken only when siphons could not be located within a given marsh. Vascular plants within the quadrat were cut off at mud level. Two to six mud samples were taken from different areas within each salt marsh or estuarine bank and transported back to the laboratory on ice.

In the laboratory, each sample was observed under the microscope for gametangia. Then, each sample was subdivided into quarters, placed into deep culture vessels and filled to one-half of the mud sample thickness with culture media. During the early years of the study, the divided crude cultures were placed in enriched seawater Grund medium (von Stosch, 1969) and then incubated in Hotpack No. 352642 growth chambers with set photoperiods of 8L:16D, 12L:12D or 16L:8D at 5° or 15°C temperatures. Because all of the collected species produced gametangia at least during the longest daylength and warmer temperature, beginning in 1987 we standardized culture conditions with a photoperiod 16L:8D, light intensity ca. 125 $\mu mol/m^2/sec.$, and temperatures of 15°C during the light cycle and 13°C in the dark cycle. We also varied the salinity in the crude cultures (0.3, 2.0, 4.0, 6.5, 16.0, 30.0 ppt) using modified ASP-V media (Entwisle, 1988). Additionally, mud cores of some of these cultures were subcultured into the same salinity media with 1.75% agar added. Agar cores were removed with a 0.5 cm cork borer and replaced with the same sized mud-*Vaucheria* core. The Petri dishes were sealed with Parafilm®. Microscopical observations on each crude and agar culture were made every three to four days. Drawings were made with the aid of a Zeiss camera lucida, and vouchers of each of the species are deposited in Herbarium C. W. Schneider at Trinity College, Hartford.

## RESULTS AND DISCUSSION

All nine species and one variety of *Vaucheria* presently reported from New England have been found in Connecticut marine and brackish water environments along Long Island Sound, with several of the species appearing together in the same small quadrat

of mud collected from a particular salt marsh or estuarine bank. Many of the mud samples taken without visible *Vaucheria* were found to produce siphons after incubation in culture media. Either siphons existed within the mud below grade, or dormant zygotes or asexual spores were coaxed into germinating under favorable culture conditions. Few of the crude cultures produced vegetative siphon growth without ultimately developing gametangia, and many cultures produced two to four species over time in a single quadrat. Several collecting sites, in particular those closest to large industrial cities such as Norwalk, Bridgeport, and New Haven, never produced *Vaucheria*; but on the whole, the genus is readily collected throughout the year and the coastal region of the state. None of the species presented characteristics which differ from Massachusetts populations, so the reader is referred to Blum (1972) or Christensen (1987) for descriptions including pertinent measurements. New records for Connecticut are noted with asterisks (*).

## VAUCHERIACEAE Dumortier 1822, p. 71

### *Vaucheria arcassonensis P. J. L. Dangeard 1939, p. 216.

Figures 2a, b

This species was previously known in New England only from Maine and Massachusetts (Blum and Conover, 1953; Webber, 1968). In Connecticut, it was one of the two most frequently encountered species. To the south, *Vaucheria arcassonensis* is the most abundant *Vaucheria* species in North Carolina (Ott and Hommersand, 1974), and despite extensive investigations in the Gulf of Mexico, it has been found only at a single locality in Wakulla Co., Florida (Pecora, 1980). We find *V. arcassonensis* throughout the state, fruiting during the winter-spring period, very commonly in the same samples with *V. coronata* and on occasion with *V. intermedia, V. minuta,* and *V. velutina*. Similarly, in the British Isles *V. arcassonensis* is generally mixed with *V. intermedia* and often associated with *V. coronata* and *V. velutina* (Christensen, 1987).

TYPE LOCALITY: France

DISTRIBUTION: Nova Scotia, New England, North Carolina, Florida Gulf coast, Europe, Australia.

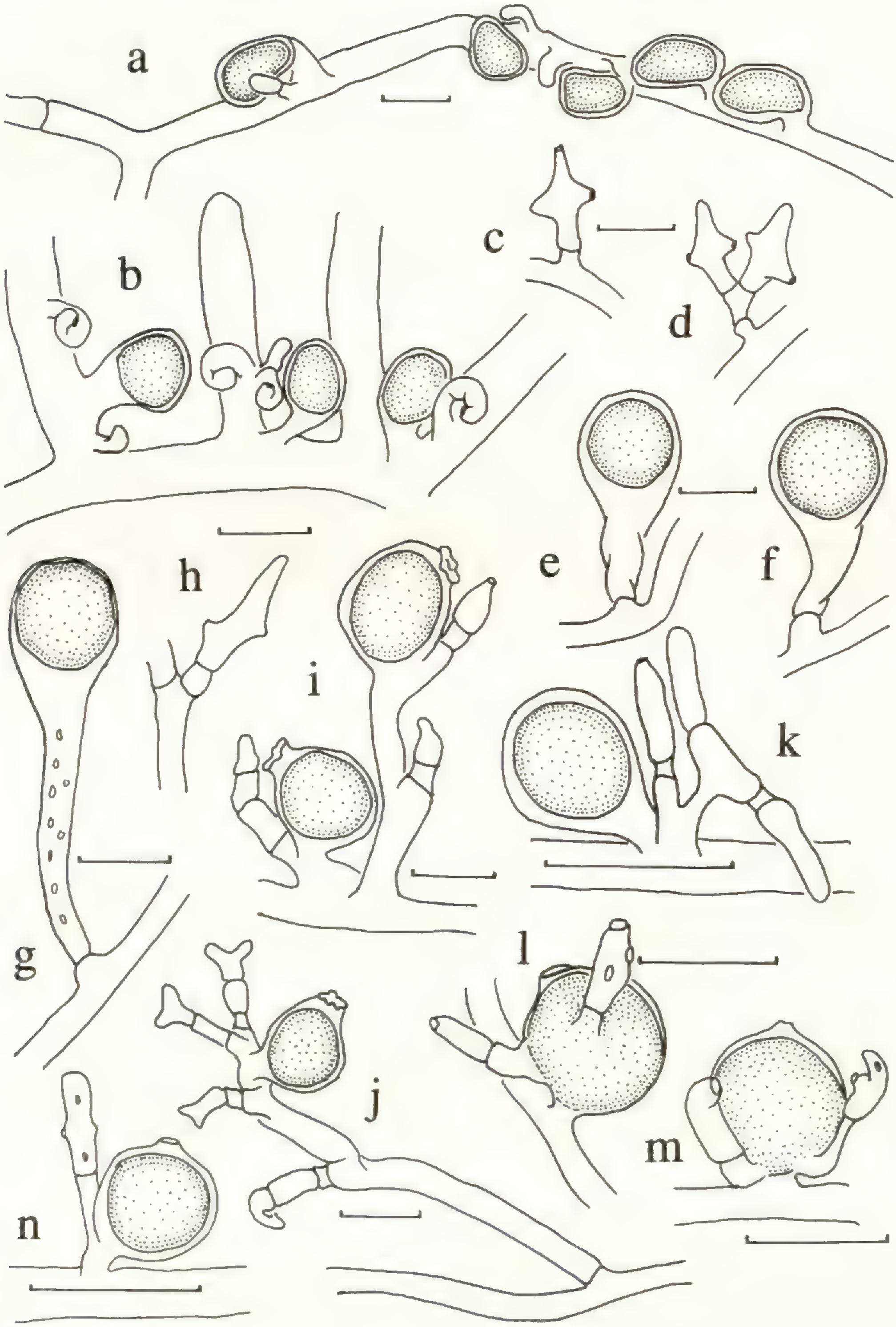


Figure 2. Connecticut marine and brackish water *Vaucheria* species, all scale bars = 100 μm: a–b. *V. arcassonensis*; a, JCV coll. Sept. 1982; b, HMW coll. Jan. 1992. c–f. *V. compacta,* OSP coll. Oct. 1991; c–d, antheridia, e–f, oogonia. g–h. *V. compacta* var. *koksaokensis,* BOL coll. Feb. 1981; g, oogonium; h, antheridium. i–j. *V. coronata*; i, HMW coll. Jan. 1992; j, PBW coll. Apr. 1983. k–n. *V. inter-*

COLLECTIONS: Fairfield Co.—23 Mar. 1981, **CIP**, *T. Roche,* fertile in culture 20 Apr. 1981; 23 Mar. 1981, **GPP**, *T. Roche,* fertile 8 Apr. 1981. New Haven Co.—23 Sept. 1982, **JCV**, *S. Heminway,* fertile 28 Feb. 1983; 3 Apr. 1983, **JCV**, *S. Heminway,* fertile 18 Apr. 1983; 1 Mar. 1992, **CGH**, *J. Cahill,* fertile in field. New London Co.—30 Nov. 1982, **PBW**, *S. Heminway,* fertile 20 Apr. 1983; 29 Jan. 1992, **HMW**, *L. MacDonald,* fertile 6 Feb. 1992; 27 Feb. 1992, **PBW**, *J. Cahill,* fertile 1 Mar. 1992; 17 Mar. 1992, **PBW**, *L. MacDonald,* fertile in field; 6 May 1992, **HMW**, *C. Schneider,* fertile 13 May 1992; 6 May 1992, **PBW**, *J. Cahill,* fertile 13 May 1992.

VAUCHERIA COMPACTA (Collins) Collins ex W. R. Taylor 1937, p. 226. Figures 2c–f

This species was previously reported in New England from Massachusetts (Blum and Conover, 1953; Webber, 1975) and Connecticut (as *Vaucheria piloboloides,* Collins 1900). We commonly found *V. compacta* in the same mud samples as *V. velutina* and occasionally with *V. intermedia* and *V. minuta.* In our cultures, *V. compacta* was fertile from 0.3–30 ppt salinity. This species is only known from very low salinity brackish water in Louisiana (2.2 ppt; Pecora, 1977), but elsewhere is found in higher salinity environments as well (Blum, 1972; Simons, 1974; Christensen, 1988).

TYPE LOCALITY: Massachusetts
DISTRIBUTION: Nova Scotia, New England, Louisiana, Europe.

COLLECTIONS: New Haven Co.—29 Sept. 1984, **CGH**, *P. Renaud,* fertile in culture 1 Mar. 1985. Middlesex Co.—5 Mar. 1987, **GRV**, *B. Bothwell,* fertile 4 Apr. 1987; 22 Sept. 1991, **GRV**, *J. Cahill,* fertile 1 Oct. 1991. New London Co.—19 Feb. 1981, **RNS**, *T. Roche,* fertile 11 June 1981; 18 Aug. 1984, **HMW**, *P. Renaud,* fertile 11 Sept. 1984; 29 Sept. 1984, **HMW**, *P. Renaud,* fertile 26 Oct. 1984; 28 Oct. 1984, **HMW**, *P. Renaud,* fertile 22 Jan. 1984; 15 Oct. 1991, **OSP**, *L. MacDonald,* fertile 2 Nov. 1991; 12 Sept. 1992, **HMW**, *H. Miller,* fertile 4 Nov. 1992.

*VAUCHERIA COMPACTA var. KOKSOAKENSIS Blum et Wilce 1958, p. 286. Figures 2g, h

This variety was differentiated from the typical form of *Vaucheria compacta* due to its greatly elongated oogonia (Blum and Wilce,

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*media*; k, GRV coll. Sept. 1991; l–m, HMW coll. Oct. 1980; n, RNS coll. Oct. 1980.

1958). To date, we have discovered this taxon only along the muddy banks at the mouth of the Blackhall River in Old Lyme, a habitat physically if not environmentally similar to that of the type locality at the mouth of the Koksoak River near Ungava Bay. Only one previous collection of *V. compacta* var. *koksoakensis* has been reported for New England, that from an Ipswich, Massachusetts salt marsh (Webber, 1968), thus our record represents a new southern limit of distribution for the entity.

TYPE LOCALITY: Quebec
DISTRIBUTION: Eastern Canada, Massachusetts, Connecticut.

COLLECTION: New London Co.—18 Feb. 1981, **BOL**, *T. Roche,* fertile in culture 10 June 1981.

*VAUCHERIA CORONATA Nordstedt 1879, p. 177. Figures 2i, j

This species was previously known only from Maine and southern Massachusetts in New England, (Blum and Conover, 1953). We have collected this alga with its diagnostic "crowned oogonia" from several localities across the state, commonly in the same mud quadrats as *Vaucheria arcassonensis,* and occasionally with *V. intermedia* and *V. minuta.* It has been collected fertile in the field from March–May. Although it thrives in higher salinities (Christensen, 1988), at its southern-most habitat for North America in Louisiana, Pecora (1980) only found *V. coronata* in 3.0 ppt salinity.

TYPE LOCALITY: Sweden
DISTRIBUTION: Greenland, Nova Scotia, New England, Virginia, North Carolina, Louisiana, Europe.

COLLECTIONS: Fairfield Co.—23 Mar. 1981, **CIP**, *T. Roche,* fertile in culture 20 Apr. 1981. New Haven Co.—1 Mar. 1992, **CGH**, *J. Cahill,* fertile 13 Mar. 1992. New London Co.—30 Nov. 1982, **PBW**, *S. Heminway,* fertile 20 June 1983; 1 May 1983, **HMW**, *S. Heminway,* fertile in field; 29 Jan. 1992, **HMW**, *L. MacDonald,* fertile 19 Feb. 1991; 27 Feb. 1992, **PBW**, *L. MacDonald,* fertile 1 Mar. 1992; 17 Mar. 1992, **PBW**, *C. Schneider,* fertile in field.

*VAUCHERIA INTERMEDIA Nordstedt 1879, p. 179. Figures 2k–n

This alga has previously been collected from New England only in Massachusetts (Blum and Conover, 1953; Webber, 1968). We

have found *Vaucheria intermedia* only on the eastern half of the Connecticut coastline, from Grove Beach to Waterford, where it is often a dominant species, at times intermixed with *V. arcassonensis, V. coronata* and/or *V. velutina.* Blum and Conover (1953) found *V. intermedia* in a habitat with a known wide range of salinities in Massachusetts from fresh water to full-strength seawater.

TYPE LOCALITY: Sweden
DISTRIBUTION: Nova Scotia, New England, North Carolina, California, Washington, Europe.

COLLECTIONS: Middlesex Co.—22 Sept. 1991, **GRV**, *J. Cahill,* fertile in culture 7 Oct. 1991. New London Co.—2 Oct. 1980, **PBW**, *T. Roche,* fertile 16 Feb. 1981; 2 Oct. 1980, **RNS**, *T. Roche,* fertile 18 Feb. 1981; 18 Feb. 1981, **BOL**, *T. Roche,* fertile 10 June 1981; 19 Feb. 1981, **RNS**, *T. Roche,* fertile 11 June 1981; 30 Nov. 1982, **PBW**, *S. Heminway,* fertile 8 Dec. 1982; 12 Sept. 1992, **HMW**, *H. Miller,* fertile 4 Nov. 1992; 9 Dec. 1992, **PBW**, *B. Stockton,* fertile 22 Dec. 1992.

## VAUCHERIA LITOREA C. Agardh 1823, p. 463. Figures 3a–c

Although this species was previously reported for Connecticut as early as the turn of the century (Collins, 1900), we found *Vaucheria litorea* to be one of the more rarely collected species, only finding it within the last two years of the study in Saybrook Point salt marsh at the mouth of the Connecticut River. Here it was found in the same mud samples with *V. compacta* and *V. velutina.* In neighboring Rhode Island, only trace amounts of this alga were found in open ocean and estuarine habitats (Villalard-Bohnsack et al., 1988).

Along the Atlantic coast, *Vaucheria litorea* is established in salt marshes and brackish ponds (Blum, 1972; Ott and Hommersand, 1974), but in the Gulf of Mexico it is characteristic of low salinity areas and habitats that are only infrequently flooded with brackish water, areas with 1.0–2.6 ppt (Pecora, 1977).

TYPE LOCALITY: Denmark
DISTRIBUTION: Nova Scotia, New England, New York, New Jersey, North Carolina, Gulf of Mexico, Washington, Europe, Australia.

COLLECTION: New London Co—15 Oct. 1991, **OSP**, *L. MacDonald,* fertile in culture 2 Nov. 1991.

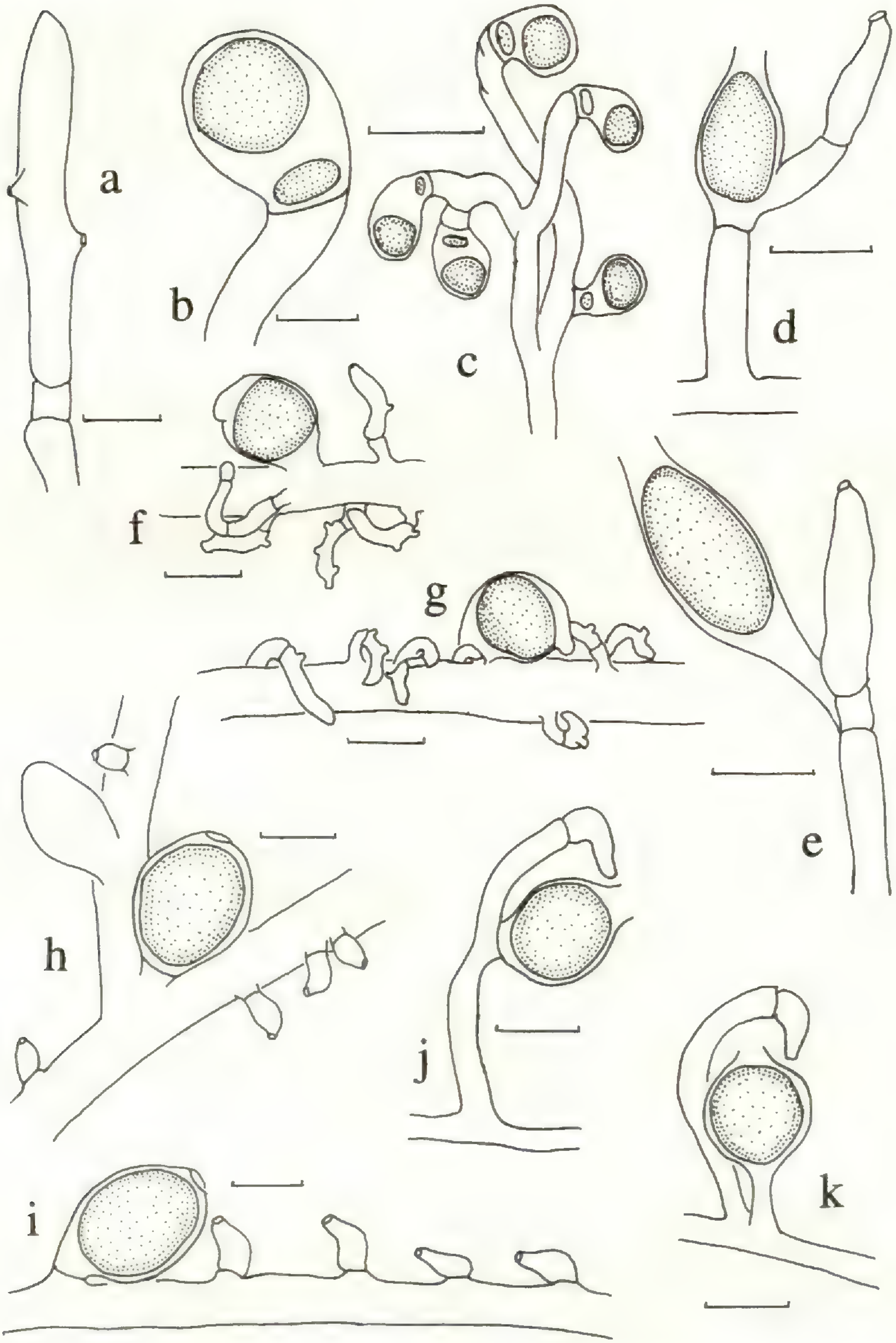


Figure 3. Connecticut marine and brackish water *Vaucheria* species, scale bars = 100 μm unless otherwise noted: a–c. *V. litorea,* OSP coll. Oct. 1991; a, antheridium; b–c, oogonia; c, scale = 500 μm. d–e. *V. minuta,* JCV coll. Sept. 1982, scales = 50 μm. f–g. *V. nasuta,* PBW coll. Feb. 1992. h–i. *V. velutina*; h, GRV

*VAUCHERIA MINUTA Blum et Conover 1953, p. 399.
Figures 3d, e

Originally described from Great Pond, Falmouth, Massachusetts, this alga was otherwise only known in New England from Maine (Blum and Conover, 1953; Webber, 1968). In Connecticut, we only infrequently found *Vaucheria minuta* along the eastern half of the coastline. Because of its small size, Ott and Hommersand (1974) suggested that this alga was perhaps overlooked and overshadowed by larger *Vaucheria* species in the same habitats. This could help account for the small number of collections in our study, as each collection of *V. minuta* in our mud quadrats was associated with *V. arcassonensis, V. compacta, V. coronota,* and/or *V. velutina.*

Blum and Conover (1953) discovered fruiting in a narrow range of natural marsh salinities 26–30.2 ppt. In culture, we found *Vaucheria minuta* with gametangia throughout the range of salinities tested, 0.3–30.0 ppt. Christensen (1988) had reported growth of this species in European populations between 2.5–40 ppt in liquid culture, with gametangia from 12.5–25 ppt. In that our cultures presumably included residual salts within the crude mud samples, we cannot state that the salinities in the muds from which our plants grow were in fact the same as the media applied to them (see following discussion on Salinity Culture Studies), thus fertility in the lowest salinity media may be misleading.

TYPE LOCALITY: Massachusetts
DISTRIBUTION: New England, North Carolina, Europe.

COLLECTIONS: New Haven Co.—23 Sept. 1982, **JCV**, *S. Heminway,* fertile in culture 2 Mar. 1983. New London Co.—29 Sept. 1984, **HMW**, *P. Renaud,* fertile 15 Apr. 1985; 29 Jan. 1992, **HMW**, *J. Cahill,* fertile 19 Feb. 1992; 6 May 1992, **HMW**, *C. Schneider,* fertile 13 May 1992.

*VAUCHERIA NASUTA W. R. Taylor et Bernatowicz 1952, p. 408. Figures 3f, g

Prior to this study, *Vaucheria nasuta* was reported from New England only in Barnstable Marsh on Cape Cod (Bernatowicz,

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coll. Sept. 1991; i, RNS coll. Oct. 1980. j–k. *V. vipera,* JCV coll. Sept. 1982, scales = 25 μm.

1958) and two sites in Gloucester, Massachusetts (Webber, 1976). Webber (1976) found this species growing on the *Spartina* leaf litter at the separation of the lower and upper salt marsh. We found this species in one salt marsh; a small, protected habitat along the bank of a tidal channel behind Pleasure Beach, Waterford, underneath *Spartina* and intermixed with populations of *V. arcassonensis, V. coronata,* and *V. velutina* in the same mud quadrat. Although *V. nasuta* is apparently uncommon in New England, it is the second most abundant species along the North Carolina coast after *V. arcassonensis* (Ott and Hommersand, 1974). Blum reported this alga from California in 1971, the only known non-Atlantic Ocean site.

TYPE LOCALITY: Bermuda
DISTRIBUTION: New England, North and South Carolina, Bermuda, Gulf of Mexico, California.

COLLECTIONS: New London Co.—27 Feb. 1992, **PBW**, *J. Cahill,* fertile in culture 1 Mar. 1992; 17 Mar. 1992, **PBW**, *L. MacDonald,* fertile in field.

VAUCHERIA VELUTINA C. Agardh 1824, p. 312. Figures 3h, i

In New England, this alga is known from all of the coastal states except New Hampshire (as *Vaucheria thuretii,* Farlow, 1881; Collins, 1900; Blum, 1972; Villalard-Bohnsack et al., 1988). *V. velutina* is widespread in North America and the most commonly encountered species in the Gulf of Mexico, where it grows in salinities from 2–35 ppt (Pecora, 1977, 1980). In Connecticut, we also find it more frequently in salt marshes throughout the state than any other *Vaucheria* species, and at the full range of salinities tested. *V. velutina* was nearly always found growing in the same mud quadrats with *V. compacta,* and also with all of the other species except *V. litorea,* thus paralleling intrageneric associations in Europe (Christensen, 1987).

TYPE LOCALITY: France
DISTRIBUTION: New Brunswick, New England, New Jersey, North Carolina, Florida, Gulf of Mexico, Washington, British Columbia, Iceland, Europe, West Africa, Indian Ocean, Asia, Hawaii, Australia.

COLLECTIONS: Fairfield Co.—23 Feb. 1985, **SHI**, *P. Renaud,* fertile in culture 30 Apr. 1985. New Haven Co.—23 Sept. 1982, **JCV**, *S. Heminway,* fertile 11 Oct.

1982; 29 Sept. 1984, **CGH**, *P. Renaud,* fertile 29 Jan. 1985; 5 Mar. 1987, **SVM**, *B. Bothwell,* fertile 12 Mar. 1987; 1 Mar. 1992, **CGH**, *L. MacDonald,* fertile 17 Mar. 1992. Middlesex Co.—5 Mar. 1987, **IRC**, *B. Bothwell,* fertile 4 Apr. 1987; 5 Mar. 1987, **GRV**, *B. Bothwell,* fertile 4 Apr. 1987; 22 Sept. 1991, **GRV**, *J. Cahill,* fertile 1 Oct. 1991; New London Co.—2 Oct. 1980, **HMW**, *T. Roche,* fertile 10 Mar. 1981; 2 Oct. 1980, **RNS**, *T. Roche,* fertile 18 Nov. 1980; 18 Aug. 1984, **HMW**, *P. Renaud,* fertile 7 Sept. 1984; 29 Sept. 1984, **HMW**, *P. Renaud,* fertile 5 Oct. 1984; 3 Mar. 1987, **HMW**, *B. Bothwell,* fertile 4 Apr. 1987; 27 Feb. 1992, **PBW**, *J. Cahill,* fertile 19 Mar. 1992; 12 Sept. 1992, **RNS**, *B. Stockton,* fertile 21 Sept. 1992.

VAUCHERIA VIPERA Blum 1960, p. 298. Figures 3j, k

Previously reported from Bridgeport, Connecticut along with the type collection from Barnstable Harbor, Cape Cod and South Essex, Mass. (Blum, 1960), *Vaucheria vipera* has not been reported since in North America, although it has been discovered in Europe and Asia (Simons and Vroman, 1968). We collected it only once, in a salt marsh off Trolley Road, Sachem Head at Joshua Cove, Guilford, from the high intertidal banks of the tidal inlet approximately 17 m from the cove on compacted sediment covered with cyanobacteria and sparse *Spartina.* This habitat would have been inundated at high tide with full-salinity seawater, especially during times of low precipitation. Blum (1960) found this delicate species mixed with either *V. compacta* and *V. velutina* (as *V. thuretii*) and the Joshua Cove population shares its habitat with *V. minuta* and *V. velutina.*

TYPE LOCALITY: Massachusetts
DISTRIBUTION: New England, Europe, Japan, Hong Kong.

COLLECTION: New Haven Co.—23 Sept. 1982, **JCV**, *S. Heminway,* fertile in culture 8 Oct. 1982.

## SALINITY CULTURE STUDIES

All of the mud quadrats collected within the last two years were subdivided and cultured in media with salinities of 0.3, 2.0, 4.0, 6.5, 16.0, and 30.0 ppt. Because the technique consisted of placing estuarine mud samples in culture vessells and then subjecting them to culture media with various salinities, the effective salinity of a culture did not take into account the native salts within each mud sample. Nevertheless, the wide range in salinity of the media

into which the mud was inoculated was expected to account for some differences in a particular species' ability to reproduce. Although some species from local populations indeed did not produce gametangia in culture at all salinities, at least one population of *Vaucheria arcassonensis, V. compacta, V. litorea, V. nasuta,* and *V. velutina* was found reproductive in all of the salinity media. Although they produced gametangia during the earlier years of the study in the enriched seawater Grund medium, *V. coronata* and *V. intermedia* were never identified in the 30.0 ppt salinity ASP-V medium despite producing abundant reproductive structures in subdivided samples at all of the other salinities. Christensen (1988) successfully cultured both species at a wide range of salinities and reported gametangia for *V. intermedia* between 0–40.0 ppt and *V. coronata* between 7.5–30.0 ppt. *V. minuta* was identified in all except the 4.0 ppt salinity medium, but this was considered an artifact of data collection as this very delicate species was found in all lower and higher salinities and, because of its size, could easily be overlooked in cultures of mixed species.

Subcultures from the crude samples invariably produced agar-penetrating siphons within the Petri dishes, with excellent growth at all salinities. After more than a week, all of the cultures initiated the production of numerous aplanospores, and many of these quickly germinated *in situ.* In the third or fourth week after inoculation into the agar media, gametangia were finally observed for three species, *Vaucheria arcassonensis, V. compacta,* and *V. coronata.* Because more than one species was found in most of the agar dishes and all three species have overlapping siphon diameters (Blum, 1972), we cannot, therefore, presume that aplanospores were produced by all three species. Christensen (1987), however, reported aplanospores of *V. compacta* forming under culture conditions, yet he rarely collected them in the field together with the identifying gametangia. Christensen also added that asexual spores of *V. arcassonensis* and *V. coronata* were unknown.

ACKNOWLEDGMENTS

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# *VAUCHERIA SUBSIMPLEX* CROUAN FROM A MASSACHUSETTS SALT MARSH: FIRST UNITED STATES RECORD

EDGAR E. WEBBER

## ABSTRACT

*Vaucheria subsimplex* Crouan has been collected from a salt marsh at Gloucester, Massachusetts. This report appears to be the first citation of this species in the United States, and it is the second in North America. At Gloucester, *Vaucheria subsimplex* and *V. velutina* occur as a "zone" at MHW in the mud of tidal creek banks, these algae forming gametangia throughout the summer. Ecological observations of the Gloucester material compare favorably with similar data about *V. subsimplex* from European and Scandinavian salt marshes.

Key Words: *Vaucheria,* salt marsh, Massachusetts

## INTRODUCTION

Prior to 1960, the only paper dealing with the botany of Massachusetts salt marshes was that of Chapman (1940), which emphasized the biology of seed plants at a marsh in the town of Saugus. Indeed, field studies of marine algae at that time had not dealt specifically with the salt marsh habitat, but centered about the vegetation of open coasts in temperate regions of the world. Such paucity of algal research in salt marshes prompted field and laboratory studies emphasizing benthic algae in an extensive salt marsh-estuary complex at Ipswich, MA (e.g., Wilce et al., 1970; Webber and Wilce, 1971).

*Vaucheria* species are among the most conspicuous algae in New England salt marshes. Their massed threads commonly form green to greenish-black "turfs" on mud and marine peat substrata. Despite their prevalence, only 4 species of *Vaucheria* were known from New England salt marshes before 1953. At this time, reports by Blum and Conover (1953), and later by Blum (1960) and Webber (1968), resulted in 10 *Vaucheria* taxa recognized from Massachusetts salt marshes. The taxa are: *V. compacta* (Collins) Collins; *V. litorea* C. Ag; *V. piloboloides* Thur.; *V. velutina* C. Ag.; *V. arcassonensis* Dangeard; *V. coronata* Nord.; *V. intermedia* Nord.; *V. minuta* Blum and Conover; *V. vipera* Blum; *V. compacta* (Collins) Collins var. *koksoakensis* Blum and Wilce. An additional species, *V. nasuta* Taylor and Bernatowicz, was collected from a salt marsh in Gloucester (Webber, 1976). I have

since found *V. nasuta* in abundance at a Yarmouthport salt marsh (Cape Cod), and recently it was located for the first time in Connecticut (Schneider et al., p. 108).

## MATERIALS AND METHODS

During August, 1987, collections of *Vaucheria* were made in the Cape Ann region of Massachusetts. The type locality for *V. vipera* in Essex, and a small salt marsh immediately behind Gloucester Harbor were chosen as collecting sites. At Essex, samples were taken from the mud banks of a tidal creek, as well as from a poorly drained section of the marsh populated by *Salicornia europaea* L. From the marsh at Gloucester, *Vaucheria* was evident both on creek bands and on the muddy soil beneath *Spartina alterniflora* Loisel.

Collections were returned to Keuka College, Keuka Park, NY, and kept in petri plates under ambient day/night periods for several additional days until green "tufts" arising from the mud were apparent. At this time, small portions of this new growth were placed in sterile petri dishes containing Erd-Schreiber medium (Provasoli et al., 1957). The algae were then grown in a culture chamber at 16°C under constant light, the dishes being approximately 10 cm below a 20 W cool fluorescent light. Fresh medium was added at weekly intervals, and all cultures were examined microscopically at this time.

## RESULTS AND DISCUSSION

Nine days after inoculation, antheridia and oogonia formed on the *Vaucheria* from the Essex creek banks, and two species, *V. vipera* and *V. velutina,* were identifiable.

Collections of mixed *Vaucheria* species are common. Because of this mixing, it is important to maintain cultures until all the algae have reached a sexual reproductive condition, i.e., until all species from the mix are identified.

For example, in a Gloucester site collection, two weeks after initial inoculation, *V. litorea* was abundantly reproductive. The algae were removed, preserved in a 3% formalin-sea water mixture, and the vegetative material was left in the petri dish. On September 15, 1987, 45 days after initial inoculation, these *Vaucheria* threads became reproductive. Upon microscopic ex-

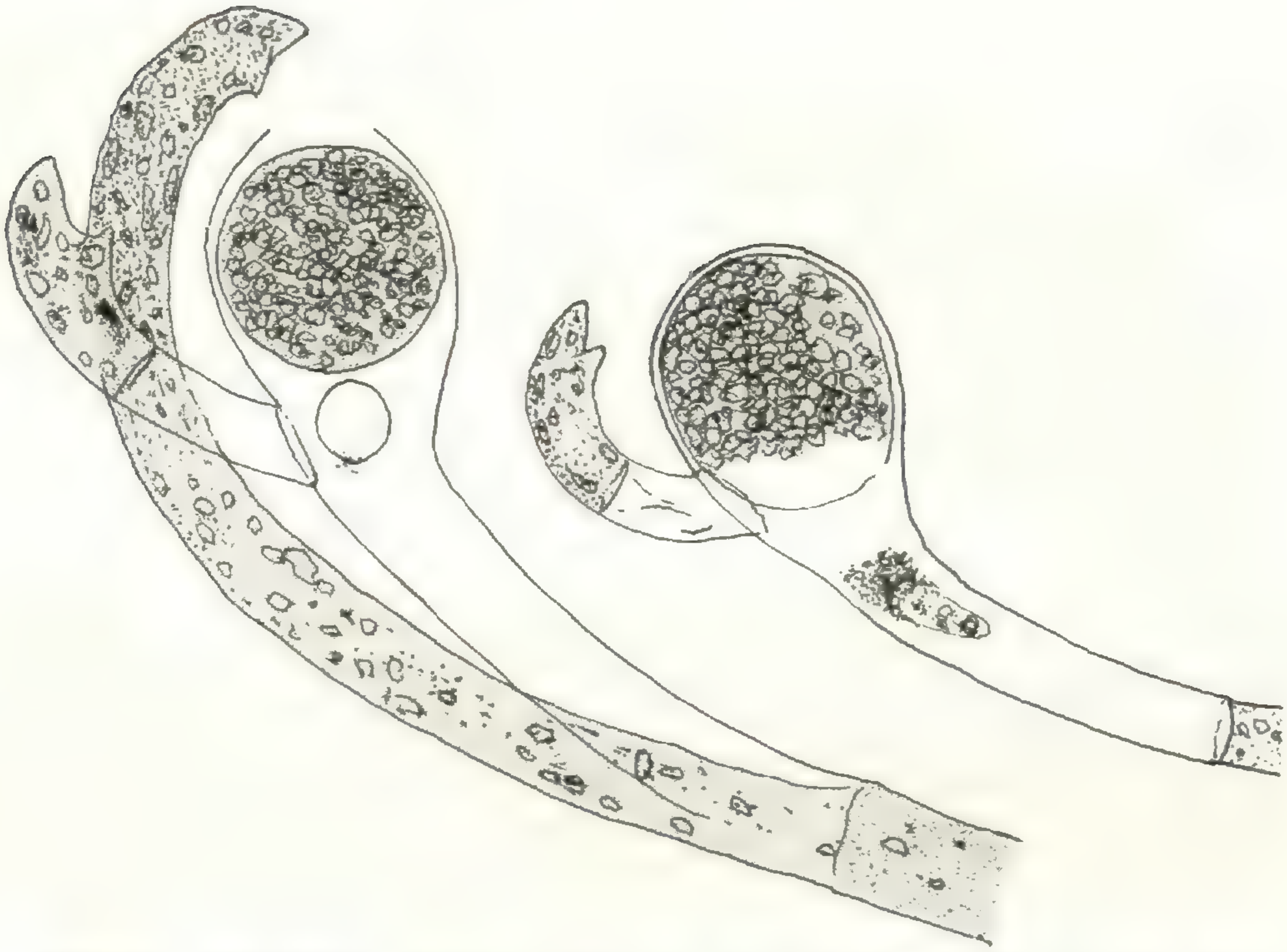

Figure 1. *Vaucheria subsimplex* Crouan showing the typical terminal gametangia with the antheridia characteristically in an arc toward the oogonia. Material collected from a salt marsh, Gloucester, MA, in summer, 1987. Drawing by Dr. John Blum. Magnification 150×.

amination, the algae were identifiable as *Vaucheria subsimplex* Crouan. At this time, other cultures from the same field location also contained *V. subsimplex* (Figure 1).

*Vaucheria subsimplex* is of common occurrence in European salt marshes. The Gloucester, MA record appears to be the first record of this species in the United States, and it is the second in North America. The first report of *V. subsimplex* in North America was based on material from Ungava Bay, Quebec (Blum and Wilce, 1958).

The Gloucester and Essex, MA locations were re-visited in early June, 1992, and additional *Vaucheria* collections were taken. Culture conditions for these collections were the same as described in METHODS. On June 18, *V. subsimplex* was located in one collection from the Gloucester tidal creek banks. Mixed with this species was *V. velutina,* which also appeared in other collections from this site. Thus, a *V. subsimplex*/*V. velutina* "zone" exists on the Gloucester mud creek banks at MHW level. Small amounts of *V. nasuta* also appeared in these and additional collections from this "zone."

The prevalence of a summer reproductive *Vaucheria subsimplex/V. velutina* mixture on tidal creek banks at MHW has been reported from the Netherlands (e.g., Nienhuis and Simons, 1971; Polderman, 1975b). In another study, Polderman (1975a) cited the winter and autumn as prime reproductive times for *V. subsimplex.* Also, according to Simons and Vroman (1973), *Vaucheria subsimplex* and *V. velutina* are "summer species" growing mostly on the seaward edges of shores on hydrogen sulfide containing substrata where soil moisture and salinity are high. These same authors (1968) stated that *V. subsimplex* may also reproduce sexually to a lesser degree in winter and spring. Winter data from Gloucester concerning the reproduction of this species is not available, but *V. subsimplex* readily forms gametangia during the summer in Massachusetts.

Salinity levels at the Gloucester site appear high. Salinities from a site approximately 100 meters seaward from the above location show a range from 22‰ to 29‰, with extremes of 17‰ and 31‰ (Mass. Audubon Soc., 1990). In laboratory experiments (Christensen, 1988) *Vaucheria subsimplex* showed maximum growth at 22‰, and gametangia were formed between 10 to 30‰, thus supporting his field observations that *V. subsimplex* occurs in sites of "constant and high salinity."

In addition to being a component of the *Vaucheria subsimplex* "zone" at Gloucester, *V. velutina* is common also at Essex and deserves further mention. Here, it is mixed with *V. vipera* and *V. compacta* and inhabits exposed sites of wet black muck in the upper littoral, subject to sea water dilution by rainfall and flooding by spring tides. Such observations suggest a euryhaline nature for *V. velutina,* which is confirmed by culture studies and its occurrence with *V. compacta* "high up in estuaries" (Christensen, 1988). Further, *V. velutina* appears to increase its vegetative mass under field conditions through abundant aplanospore production and germination (Knutzen, 1973; Simons and Vroman, 1973; Simons, 1975). Asexual reproduction by aplanospores was common in several of my *V. velutina* cultures.

## CONCLUSIONS

The first United States record for *Vaucheria subsimplex* Crouan is reported from a salt marsh at Gloucester, MA. *Vaucheria subsimplex* and *V. velutina,* admixed with small quantities of *V.*

*nasuta,* form a "zone" at MHW on tidal creek banks. Such an occurrence appears related to high moisture and salinity levels of their mud substrata. *Vaucheria subsimplex* readily forms gametangia throughout the summer; winter data concerning the reproduction of this species is not yet available. Ecological observations of *V. subsimplex* at Gloucester compare favorably with relevant data about this species from various salt marshes in Europe and Scandinavia.

## ACKNOWLEDGMENTS

I am most grateful to Dr. John L. Blum for his support and assistance during the course of this study. Sincere thanks are given to: Mr. James Dominick, Gloucester, MA for granting me access to the salt marsh where *Vaucheria subsimplex* was discovered; Dr. Donald Pfister, Curator, The Farlow Herbarium, for loaning type material of *Vaucheria sphaerospora* Nord.; Dr. William Dress, Prof. Emeritus, Bailey Hortorium, Cornell University; and to Dr. Robert Buchsbaum, Massachusetts Audubon Society. Particular appreciation is expressed also to Drs. Robert Wilce and Crag Schneider for their constructive critiques of this manuscript.

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# THE IDENTITY OF *ERYTHRONIUM BRACTEATUM* (LILIACEAE)

BRIAN MATHEW

Whilst trying recently to account for all the epithets which have been published in the genus *Erythronium* I encountered the question of the identity of '*Erythronium bracteatum*' Bigelow. Homer D. House, in his Annotated List of the Ferns and Flowering Plants of New York State (1924) gives *E. bracteatum* as a synonym of *E. americanum* and, although I had no particular reason to doubt this opinion, I felt that a sight of the type specimen would be of interest, in view of this curious epithet in a genus which does not normally possess bracts on its inflorescences.

The entry in Index Kewensis for this epithet gives the author and place of publication as Bigelow in Beck, Bot. 365 = *albidum.* This refers to Lewis C. Beck, Botany of the Northern and Middle States (1833), and a check on page 365 reveals that the plant was collected on 'high mountains, Ver.' Beck did provide a description of the plant and attributed the name to Bigelow, but without a literature reference to Bigelow's involvement with the name. The obvious place to start a search for any such involvement was in Bigelow's Florula Bostoniensis. The first edition proved to be of no help but the second, published in 1824, revealed that the species was in fact validly published with Latin and English descriptions and a type citation; Bigelow acknowledged that Boott actually provided the name: 'discovered by Mr. Boott — — — and by him designated by the foregoing name.'

The full citation for the species is:

**Erythronium bracteatum** Boott ex Bigelow, Fl. Boston. ed. 2:136(1824). TYPE: USA, Vermont, Camel's Rump mountain, June, *Boott* (holotype K!).

Bigelow provides the following description: 'Leaves very unequal, the primary one being two or three times as large as the secondary. Scape shorter than the leaves with a narrow lanceolate bracte about an inch long, situated an inch or two below the flower. Corolla yellow, half as large as in the preceding species [ie. *E. americanum*], petals gibbous at base. Stamens half as long as the corolla. Style clavate; stigmas united?'

The description given by Beck is almost a straight repetition of that provided by Bigelow.

W. J. Hooker was also aware of this plant, although in Flora Boreali-Americana 2:182(1839) he gives no real indication that he knew of the earlier work by Bigelow, in spite of the fact that the Kew Library copy of the Florula Bostoniensis was donated to 'Professor Hooker—with the author's respects.' In a footnote to *E. albidum* Hooker states: 'I possess from Dr. Boott a very remarkable state of this plant, or a distinct species, from Vermont, U.S., *E. bracteatum* Boott, mst. The leaves are lanceolate, and taper gradually into the foot-stalk. The flower is small (¾ of an inch long), greenish, and there is a bractea on the peduncle, indicating a disposition to bear more than one flower. Only one specimen was found.' This Hooker connection provided hope that the type may in fact be in existence in the Kew herbarium, and a search through all the Erythronium folders duly revealed a specimen labelled *Erythronium bracteatum* Bigelow; the reverse of the sheet reads: 'Discovered on Camel-Rump's [presumably a mistake for Camel's Hump!] mountain near Waterbury-Vermont-U.S.A. July 14. 1817 [signed] Francis Boott. This was the only specimen I found in flower & this was faded. I was too late to find it in perfection. An accurate drawing of this was made by my friend Mrs Hardcastle which I sent to Sir J. E. Smith. [initialled] F.B.'

The Kew specimen consists of two leaves without a rootstock, and an inflorescence bearing one flower; the scape does bear a bract just beneath the flower, as observed by Bigelow, Beck and Hooker. The venation of the leaves, and of the perianth segments, is typical of *Erythronium americanum* and in the absence of any strong contenders it seems likely that *E. bracteatum* is an aberrant variant of this. The flower is not in good condition so that the internal features are difficult to observe, but it is smaller than that of *E. americanum* with segments under 2 cm in length. The flowering time, given as July 17th by F. Boott, is extraordinarily late for this species and it seems possible that something had happened to this particular individual, such as being buried by a slip of soil or rocks, or beneath a very late-melting snowpatch, causing its abnormal flowering time and morphological appearance; even the 'bract' is not very convincing and appears to be somewhat deformed.

On the evidence available I am inclined to agree with Homer

D. House, that *E. bracteatum* is a synonym of *E. americanum* Ker-Gawler.

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# *ISOETES PROTOTYPUS* (ISOETACEAE) IN THE UNITED STATES

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## ABSTRACT

*Isoetes prototypus* Britton, an endemic of the Atlantic Maritime Ecozone of Northeastern North America, is reported for the first time in the United States from Acadia National Park, Maine. It is a rare species throughout its range, being known elsewhere (in Atlantic Canada) from only five populations. For reasons of site requirements and possibly dispersal limitations, *Isoetes prototypus* is unlikely to be found in the United States away from the coastal region of Maine. It warrants designation as Critically Imperiled (G1S1) throughout its range.

Key Words: *Isoetes prototypus,* Isoetaceae, Maine, Acadia National Park, distribution, conservation

## INTRODUCTION

The rarest member of the pteridophyte genus *Isoetes* in northeastern North America is the Prototype Quillwort, *I. prototypus* Britton (Britton and Goltz, 1991). It is one of the few northeastern North American diploid *Isoetes* species (2n = 22), increasing its value for evolutionary investigations of a group in which alloploidy and autoploidy are considered to be important for speciation (Taylor and Hickey, 1992). *Isoetes prototypus* also has a variety of morphological characteristics which are rare and in some cases, unique in North American *Isoetes* (Britton and Goltz, 1991) (Figures 2 and 3).

*Isoetes prototypus* has been previously reported from only four lakes, all in Atlantic Canada.[1] A specimen representing an additional locality and constituting the first record from outside Canada was discovered in material taken in Acadia National Park, Maine. The following describes that population and considers aspects of the ecology, geography and conservation significance of the species.

[1] A fifth Canadian population has recently been rediscovered at Sandy Lake, Annapolis Co., Nova Scotia (*D. M. Britton, A. Anderson and R. Newell 12,506,* 23 August 1990, OAC).

## METHODS

A recent review of a set of *Isoetes* specimens collected in Acadia National Park, Maine resulted in the discovery of a specimen of *I. prototypus*. The site was subsequently visited and investigations of *Isoetes* population size and site ecology were undertaken. Comparison of these data with those gathered in earlier studies (e.g., Britton and Goltz, 1991) was undertaken in order to assess ecological and geographical similarities between American and Canadian populations.

## RESULTS

Despite recent surveys of most northeastern *Isoetes* material for several studies (including Kott and Britton, 1983; Taylor et al., 1993 and pers. obs. (1989–1992) in maritime Canada and New England), *I. prototypus* remained unrecorded in the United States until we identified a collection from the north end of Bubble Pond, Acadia National Park, Maine (*C. W. Greene 1782,* 18 August 1987, HCOA, OAC). A subsequent search of the site uncovered a large population of *I. prototypus* there (*D. F. Brunton and K. L. McIntosh 11,347,* 19 September 1992, OAC, DFB, CAN, DAO, MIL, BM).

Bubble Pond is a small, spring-fed lake at 101 m asl—a relatively high elevation along the coastal plain. The lake is situated in a broad Palaeozoic volcanic and intrusive bedrock trough. Its profile is characterized by a broad, shallow shelf of silty-sand/coarse sand extending 4 to 40 m out from shore which pitches steeply into much deeper, noticeably darker water (Figure 1). *Isoetes prototypus* was found growing through dense *Eriocaulon septangulare* mats in a 20–30 cm thick layer of loose, silty ooze over sand in deep cool, oligotrophic water at the top of the steep slope to deeper water. The plants were not observed in water less than 1.5–> 2.0 m deep, although label data from the 1987 collection reports that those plants were collected in water ca. 1.0 m deep.

Bubble Pond *I. prototypus* has unusually long leaves—12.5 cm (average of 15 plants)—compared to Canadian material—6.4 cm (average for 22 plants from Nova Scotia and New Brunswick). It is otherwise typical of the species (cf. Britton and Goltz, 1991) *viz,* extremely straight, stiff, sharp-pointed, lustrous, dark-green

Figure 1. North end of Bubble Pond, Acadia National Park, Maine. *Isoetes prototypus* is abundant well out from shore, from the point where water depth > 1.5 m is achieved (dark area).

leaves with mahogany-coloured bases and a velum completely covering the sporangium. Megaspores are small (< 500 μm) and ornamented by an obscure, reticulate network of low, broad, 'meandiform,' mound-like markings on an essentially smooth surface. These are typical of the megaspores of *I. prototypus* (Figure 2).

*I. tuckermanii* A. Br. occurs commonly at the north end outlet of Bubble Pond in 2 to 10 cm deep fresh, warm water on silty-sand/coarse sand flats; none was observed in deeper water. The presence of a third *Isoetes* species in Bubble Pond, *I. macrospora* Dur., is indicated by the single up-rooted plant of the hybrid *Isoetes* × *harveyi* A. A. Eat. (= *I. macrospora* × *tuckermanii*). It is a common sterile hybrid within mixed populations of the parent species and always occurs in the company of both parents (Britton, 1991). Both of these species (and their hybrid) can be readily separated from *I. prototypus* by their more delicate, recurved, reddish-green leaves and larger, intricately ornamented megaspores (high-walled, densely reticulate pattern with a band of small, more or less distinct spines along the equator—cf. Kott and Britton, 1983).

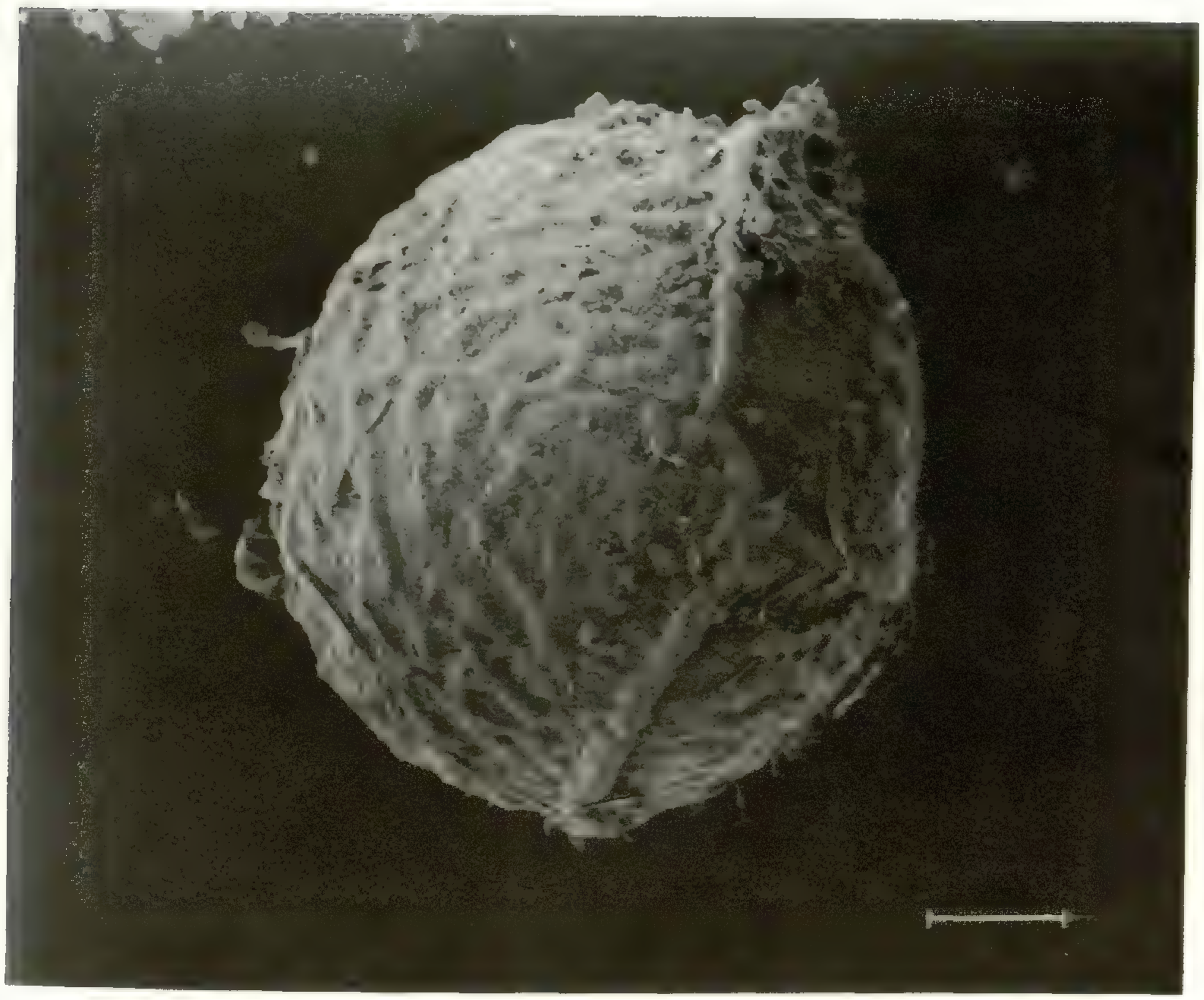

Figure 2. *Isoetes prototypus* megaspore with irregular pattern of tubercles and low, meandiform ridges (TOPOTYPE/PARATYPE, York Co., New Brunswick; *Hinds 77-41* UNB 28537) (bar = 100 μm).

This habitat is comparable to Canadian sites. First evidence of *I. prototypus* is usually offered by plants washed up on shore because the typically abundant deep water populations are not readily apparent from the surface (Britton and Goltz, 1991). Similarly, *I. prototypus* was not apparent during an unaided search from the surface of Bubble Pond. We examined that population with the aid of a glass-bottomed box to improve underwater viewing and by swimming down to the plants. We have had success in obtaining plants at other sites by dragging an anchor across the lake bottom and collecting the dislodged plants which readily float to the surface thereafter.

Evidence of *I. prototypus* was not detected in a brief survey of other apparently suitable lakes in Acadia National Park in September 1992; nearby Jordan Pond appears to be a particularly likely candidate but has received considerable botanical attention for over a century without providing evidence of this species.

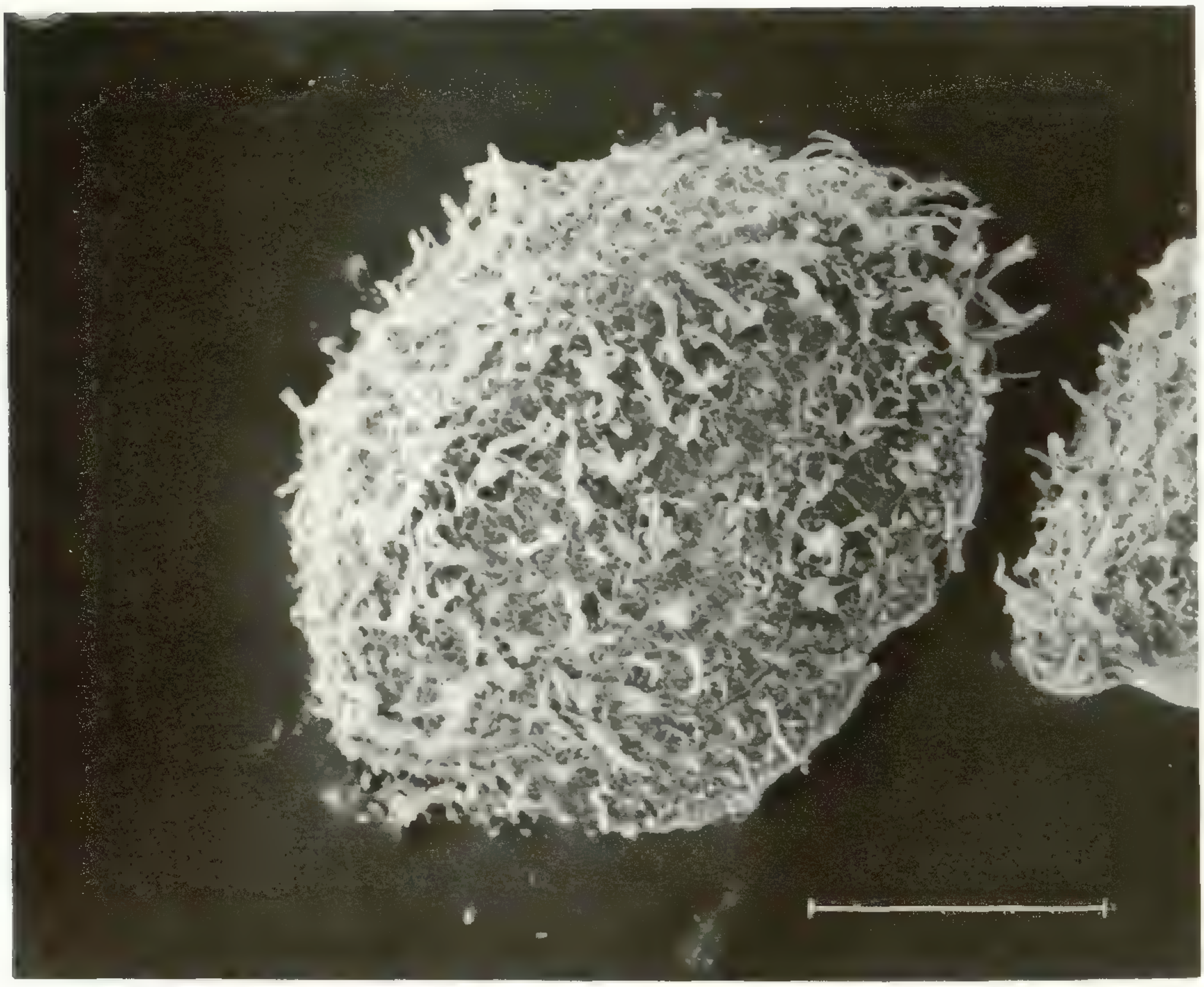

Figure 3. Densely fine-spinulose *Isoetes prototypus* microspore (TOPOTYPE/PARATYPE, York Co., New Brunswick; *Hinds 77-41* UNB 28537) (bar = 10 μm).

## DISCUSSION

Few washed-up plants were evident at Bubble Pond, in contrast to other *I. prototypus* lakes we have examined. Boating and swimming are prohibited in this lake, perhaps lessening the disturbance to the bottom by motors, fishing lines and swimmers. We also suspect that bottom-feeding waterfowl and Muskrats, wintering reptiles and amphibians, and/or spawning fish may be responsible for producing massive shore 'wracks' (accumulations of washed-up vegetation) consisting of various species of *Isoetes* plants, but this has not been confirmed. Such *Isoetes* wracks are regularly encountered along the Atlantic coast and in western North American cordillera—pers. obs.

The Bubble Pond station of *I. prototypus* constitutes the southernmost population for this endemic of the Atlantic Maritime Ecozone (cf. Wiken, 1986). Its occurrence in a deep, cold, nutrient-poor lake may reflect a particularly strict set of site requirements and/or the species' inability to tolerate significant competition.

We typically find *Isoetes prototypus* in such sites either growing alone or with very few associates (such as *Eriocaulon septangulare* With., *Isoetes macrospora* or *Isoetes* × *heterospora* A. A. Eat.).

Such a distinctive and restrictive habitat requirement likely also restricts the distributional potential of *I. prototypus*, contributing to its global rarity. Dispersal to such sites may be limited by the existence of its complete sporangial velum which reduces the ease of separation and rupture of the sporangium from the sporophyll, perhaps reducing the availability of free microspores and megaspores for transport by water currents, animal activity or other dispersal agents.

It seems likely that *I. prototypus* will remain a rare species in the United States, found only in the cold, clear Palaeozoic-bedrock based lakes in the Atlantic Maritime Ecozone along and near the Atlantic coastal plain in Maine. Given the greater intensity of botanical investigation in New England than in Atlantic Canada, it seems unlikely that evidence of commonly distributed American populations would have been missed when documentation of comparable Canadian populations dates back to the early years of this century.

The conservation status of *L. prototypus* meets the high priority designation of the Nature Conservancy ranking scheme (Morse, 1987; Argus and Pryer, 1990); the species likely warrants G1 (Critically Imperiled) status. Similarly, it warrants Critically Imperiled Provincial/State status (S1) for Nova Scotia, New Brunswick and Maine.

The rarity of populations of this species and the general vulnerability of aquatic *Isoetes* to water pollution strongly suggests that *I. prototypus* warrants Endangered (or at least Vulnerable) Species designation in both Canada and the United States.

## ACKNOWLEDGMENTS

Our thanks to congenial and expert field associates Allan Anderson and Karen L. McIntosh who have contributed a great deal to our on-site investigations throughout the range of the species. We also appreciate the opportunity of examining the Acadia National Park material afforded by Acadia National Park botanist Linda Gregory. The second author thanks the National Sciences and Engineering Research Council of Canada for a grant in aid of research.

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# *CAREX CASTANEA* × *C. DEBILIS*, A NEW NATURAL HYBRID FROM ONTARIO

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## ABSTRACT

A high level of achene sterility, non-exserted anthers, and intermediacy in qualitative and quantitative characters support the recognition of plants from the shore of Wendigo Lake in northern Ontario as *Carex castanea* × *C. debilis*, a new natural hybrid. This new taxon has prominent leaf pubescence like *C. castanea*, but relatively narrow leaves (less than 2.5 mm wide as in narrow-leaved specimens of *C. debilis*). The floral density of the spike and many other characters are more or less intermediate. This hybrid is probably scarce because of the evident edaphic isolation of its parents. A key and description are included.

Key Words: *Carex* section *Sylvaticae*, *Carex castanea*, *Carex debilis*, hybrid, Ontario, Canada, North America

## INTRODUCTION

*Carex* ×*knieskernii* Dewey, the hybrid of *C. arctata* Boott and *C. castanea* Wahl., both species in section *Sylvaticae*, is a widespread taxon and one of the better known hybrids in the genus *Carex* in North America (Cayouette and Catling, 1992), but few other hybrids involving *C. castanea* have been reported. Since *C. castanea* is conspicuously pubescent, unlike most North American species of *Carex*, and this character may be expected in its natural hybrids, the hybrids involving *Carex castanea* should be easy to recognize.

Several plants of *Carex* found along the upper, semi-wooded shore of Lower Wendigo Lake in Larder River Provincial Park, northern Ontario had leaves 1.5–2.5 mm wide and were clearly not referable to *C. castanea*, the wider leaves of which are 4.5–8 mm wide, yet they had distinctly pubescent leaves and sheaths, ovate perigynia and drooping pistillate spikes, thus suggesting a hybrid origin involving *C. castanea*. The non-exserted, poorly developed anthers and development of only four achenes from 700 pistillate flowers also suggested a hybrid origin. The purpose of the work reported here was to assess the likelihood of a hybrid origin and to provide evidence for the parentage.

## METHODS

Fifteen morphological characters (Table 1) were selected and measured in 10 specimens of each of *Carex arctata, C. castanea* and *C. debilis* from throughout Ontario. The same 15 characters were measured in 4 specimens of *C.* ×*knieskernii* from four widely separated localities in eastern North America and in four specimens of the putative *C. castanea* × *debilis* hybrid from Wendigo Lake. The length of the longest hair on a lower leaf was measured along the lower edge of the leaf. The total culm height was measured from the roots to the tip of the staminate spike. The length of the lowest peduncle was measured from the culm to the base of the spike. The lowest pistillate spike length was measured from the base of the lowest scale to the tip of the longest perigynium. Although the achenes of the putative hybrids *C. castanea* × *debilis* and *C.* ×*knieskernii* were mostly aborted, they were still partially developed and stalks could be measured.

Material measured included: for **Carex arctata**, *Calder 788, 7111, Cody 6464, Dickson & Martin 1656, Dore & Koyama 19938, Laird* 25 May 1952, *Soper & Lindsay 9659, Varga* 5 May 1982, *Wood* 29 May 1934, *Zgierska* 27 May 1985; for **Carex castanea**, *Brunton 6022, Calder 3106, 3132, Garton 2073, 7329, 11887, Jennings 14241, Lepage 38019, Lloyd* 20 June 1946, *Mayall & Cormack 151*; for **Carex castanea** × **debilis**, *Catling & Catling 91-224*; for **Carex debilis**, *Barkworth 2041, Calder 1952, 1969, 6505, Garton 4836, Gillet & Dore 7636, Hart 1490, Jenkins 4708, Moore 2609 and Watson 3859*; for **Carex** ×**knieskernii**, *Calder 3107, Johnson* 28 June 1981, *Lepage 36308, Williams, Collins & Fernald* 18 July 1902. Means and standard deviations of the characters for the different groups were compared. Additional material of all groups was examined to ensure that the samples were representative, although not necessarily fully comprehensive with respect to the variation within taxa. The key and description are based on a larger sample than that providing the basis for Table 1.

## RESULTS AND DISCUSSION

Although the sample sizes employed are small, they do cover a broad area and examination of many additional specimens suggested that the data in Table 1 were indeed representative of the 5 taxa, especially in the northern Ontario portions of their ranges.

While both *C. arctata* and *C. debilis* Michaux have inconspicuously scabrous-pubescent sheaths and *C. debilis* also often has scabrous-pubescent leaves, the pubescence of the putative hybrid was much more prominent, being 0.5–0.6 mm long on the lower leaf surface (Table 1). Of the *Carex* species occurring in the local area where the putative hybrids were found, only *C. castanea,* with longer pubescence on the lower leaf surface 0.5–0.7 mm long is comparable, and consequently *C. castanea* is almost certainly one of the parents. Among the species in the neighbourhood that possessed some characteristics of the putative hybrids were *Carex arctata, C. capillaris* L. and *C. debilis.* Considering ways in which the putative hybrids differed from *C. castanea,* the other parent would have to have relatively narrow leaves, relatively long pseudoculms, relatively long spikes, more rounded scales, relatively narrow perigynia, and relatively long-stalked achenes. The only species that satisfies all of these criteria is *Carex debilis. Carex arctata* has leaves too broad and acuminate scales (Table 1), whereas *C. capillaris* has spikes that are too short (< 2 cm long). Both *C. arctata* and *C. capillaris* have relatively short pseudoculms and achenes without stalks.

As is characteristic of hybrids, the four plants of putative *C. castanea* × *C. debilis* have some characteristics of one parent, some of the other, some unique characteristics, and many characteristics that are expressed as intermediate between the putative parents (Table 1). In leaf pubescence the putative hybrids are like *C. castanea,* whereas in sheath pubescence they tend more towards intermediacy. The perigynia are narrower than in either putative parent, possibly because of the lack of distension by well developed achenes. In the length of the pistillate spike and width of tips of the pistillate bracts, the putative hybrids are closer to *C. debilis* (Table 1). Intermediacy is apparent to a greater or lesser extent in flower number in the pistillate spike, pistillate bract length and width, achene stalk length, length and width of the staminate scale, and width of the staminate scale near the tip (Table 1). Although the short stalks of the achenes, whether the latter are developed or not, are clearly intermediate, they could be viewed as a developmental anomaly. For this reason and because developed achenes where the stalk length is most easily assessed are scarce, the intermediate stalk length is of limited value in the recognition of the hybrid.

Both putative parents occurred within 15 m of the hybrid plants.

Table 1. Minimum, maximum, mean and standard deviation for 14 characters in *Carex arctata, C. castanea, C. debilis, C. ×knieskernii* and putative *C. castanea × debilis.*

| Character (units) | *C. debilis* | | | | *C. castanea × debilis* | | | |
|---|---|---|---|---|---|---|---|---|
| | Min. | Max. | Mean | SD | Min. | Max. | Mean | SD |
| 1. Maximum leaf width (mm) | 1.5 | 5.2 | 3.30 | 1.143 | 1.6 | 2.1 | 1.80 | 0.245 |
| 2. Length of longest hair on lower leaf (mm) | 0.0 | 0.1 | 0.05 | 0.053 | 0.5 | 0.6 | 0.52 | 0.050 |
| 3. Total fertile culm height (cm) | 21.0 | 60.0 | 36.61 | 11.470 | 22.5 | 34.2 | 27.65 | 4.858 |
| 4. Lowest peduncle length (cm) | 4.5 | 13.2 | 7.52 | 2.691 | 5.2 | 9.2 | 6.92 | 1.723 |
| 5. Lowest pistillate spike length (mm) | 18.0 | 59.0 | 32.40 | 12.038 | 23.0 | 35.0 | 29.50 | 5.196 |
| 6. Lowest pistillate spike, flower number (no.) | 7.0 | 20.0 | 12.00 | 3.972 | 12.0 | 21.0 | 16.00 | 3.916 |
| 7. Third lowest pistillate bract length (mm) | 2.1 | 3.2 | 2.74 | 0.370 | 2.5 | 3.0 | 2.80 | 0.216 |
| 8. Third lowest pistillate bract width (mm) | 0.9 | 1.3 | 1.13 | 0.125 | 1.2 | 1.4 | 1.32 | 0.096 |
| 9. Third, width 0.5 mm from tip (mm) | 0.5 | 0.9 | 0.65 | 0.127 | 0.5 | 0.8 | 0.65 | 0.129 |
| 10. Perigynium length (mm) | 4.2 | 7.1 | 5.42 | 0.872 | 4.5 | 4.9 | 4.75 | 0.173 |
| 11. Perigynium, length of stipitate base (mm) | 0.1 | 0.2 | 0.14 | 0.052 | 0.0 | 0.1 | 0.05 | 0.057 |
| 12. Achene, length of stipitate base (mm) | 0.4 | 0.9 | 0.65 | 0.135 | 0.2 | 0.3 | 0.24 | 0.041 |
| 13. Third lowest staminate scale length (mm) | 3.1 | 4.2 | 3.52 | 0.305 | 4.2 | 4.5 | 4.32 | 0.150 |
| 14. Third lowest staminate scale width (mm) | 1.1 | 1.5 | 1.24 | 0.151 | 1.2 | 1.6 | 1.40 | 0.183 |
| 15. Third, width 0.5 mm from tip (mm) | 0.7 | 1.2 | 0.86 | 0.165 | 0.6 | 0.8 | 0.70 | 0.115 |

Table 1. Continued.

| Character (units) | *C. castanea* | | | | *C. ×knieskernii* | | | | *C. arctata* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Min | Max. | Mean | SD | Min. | Max. | Mean | SD | Min. | Max. | Mean | SD |
| 1. Maximum leaf width (mm) | 5.2 | 7.5 | 6.08 | 0.721 | 4.0 | 7.2 | 4.22 | 0.320 | 4.5 | 9.5 | 6.59 | 1.652 |
| 2. Length of longest hair on lower leaf (mm) | 0.5 | 0.7 | 0.56 | 0.084 | 0.2 | 0.4 | 0.37 | 0.050 | 0.0 | 0.0 | 0.0 | 0.0 |
| 3. Total fertile culm height (cm) | 40.8 | 94.5 | 55.05 | 16.114 | 37.7 | 54.0 | 43.15 | 7.358 | 39.0 | 57.1 | 47.23 | 5.515 |
| 4. Lowest peduncle length (cm) | 2.0 | 4.0 | 2.89 | 0.631 | 2.9 | 4.8 | 3.92 | 0.818 | 6.3 | 15.5 | 9.08 | 2.871 |
| 5. Lowest pistillate spike length (mm) | 16.0 | 28.0 | 20.80 | 3.824 | 24.0 | 39.0 | 31.75 | 6.946 | 33.0 | 59.0 | 45.20 | 7.641 |
| 6. Lowest pistillate spike, flower number (no.) | 17.0 | 38.0 | 25.20 | 6.460 | 18.0 | 29.0 | 25.00 | 4.830 | 15.0 | 44.0 | 27.20 | 7.969 |
| 7. Third lowest pistillate bract length (mm) | 3.0 | 3.9 | 3.50 | 0.350 | 2.7 | 3.4 | 3.02 | 0.299 | 3.0 | 4.4 | 3.56 | 0.488 |
| 8. Third lowest pistillate bract width (mm) | 1.2 | 1.7 | 1.50 | 0.169 | 1.4 | 1.6 | 1.50 | 0.082 | 1.2 | 1.8 | 1.55 | 0.158 |
| 9. Third, width 0.5 mm from tip (mm) | 0.2 | 0.5 | 0.35 | 0.085 | 0.1 | 0.5 | 0.30 | 0.183 | 0.1 | 0.3 | 0.12 | 0.063 |
| 10. Perigynium length (mm) | 4.4 | 5.3 | 4.78 | 0.282 | 3.6 | 4.8 | 4.32 | 0.550 | 3.1 | 4.4 | 3.85 | 0.450 |
| 11. Perigynium, length of stipitate base (mm) | 0.1 | 0.2 | 0.13 | 0.048 | 0.1 | 0.3 | 0.22 | 0.096 | 0.2 | 0.4 | 0.35 | 0.070 |
| 12. Achene, length of stipitate base (mm) | 0 | 0.1 | 0.09 | 0.032 | 0 | 0.1 | 0.07 | 0.050 | 0 | 0.1 | 0.02 | 0.042 |
| 13. Third lowest staminate scale length (mm) | 3.8 | 5.4 | 4.83 | 0.525 | 4.1 | 4.4 | 4.25 | 0.129 | 3.5 | 4.5 | 4.15 | 0.303 |
| 14. Third lowest staminate scale width (mm) | 1.2 | 2.0 | 1.52 | 0.248 | 1.6 | 1.6 | 1.6 | 0 | 1.2 | 1.7 | 1.5 | 0.141 |
| 15. Third, width 0.5 mm from tip (mm) | 0.3 | 0.6 | 0.47 | 0.106 | 0.6 | 1 | 0.8 | 0.182 | 0.4 | 0.9 | 0.64 | 0.158 |

Thus the circumstantial evidence for the hybrid nature of the evidently intermediate plants was strong.

In addition to characters noted in the key, this new hybrid may be distinguished from *C. ×knieskernii* by shorter fertile culms 22–34 cm high, and longer lower peduncles 5–9 cm long. *Carex × knieskernii* has fertile culms up to 54 cm tall, and lower peduncles 2.9–4.8 cm long (Table 1).

Over much of its northeastern range, *C. castanea* is a plant of alkaline soils (pH above 6.5), whereas *C. debilis* is a plant of acid substrates, usually sand or shallow soil over granitic rock. The waters of the Larder River running into Wendigo Lake have a relatively high pH (7.1 in July), but away from the shore substrates are characteristically acid, being either sand or shallow soil over bedrock. Along the shoreline, which is subject to seasonal fluctuation, many plant species occur that are characteristic of alkaline substrates, but they are evidently limited to the region below the level of the highest water. Examples include *Carex buxbaumii, Carex flava, Equisetum scirpoides, Platanthera psycodes,* and *Rhamnus alnifolia.* The *C. castanea* × *C. debilis* hybrids occurred with *Rubus pubescens* and the rare *Scirpus clintonii* in a transition from shoreline thicket dominated by *Alnus rugosa* and *Myrica gale* to mixed woods with *Abies balsamea, Picea mariana, Thuja occidentalis,* and *Betula payrifera. Carex castanea* occurred in the shrub thickets. Above this level is a characteristic acid ground flora which included *C. debilis* as well as *Clintonia borealis, Cornus canadensis, Epigaea repens, Lycopodium* spp., and *Vaccinium myrtilloides.* Consequently a rather unusual situation existed where acid substrates were adjacent to alkaline substrates, thus allowing *C. castanea* and *C. debilis,* species otherwise edaphically isolated, to come into close contact.

The following key and description of the new hybrid will enable it to be differentiated from related taxa.

KEY TO *CAREX* SECT. *SYLVATICAE* IN ONTARIO

1a. Leaf sheaths and especially blades glabrous or scabrous, the longer hairs less than 0.1 mm ..... 2
1b. Leaf sheaths and blades conspicuously hairy, the hairs 0.2–0.7 mm long ..... 3
2a. Achenes with a stalk 0.4–1 mm long ..... *C. debilis*

2b. Achenes stalkless, or stalk less than 0.1 mm long ..... *C. arctata*
3a. Achenes mostly well developed ..... *C. castanea*
3b. Achenes mostly more or less aborted ..... 4
4a. Leaves 1.5–2.5 mm wide ..... *C. castanea* × *C. debilis*
4b. Leaves 4–7.2 mm wide ..... *C.* × *knieskernii* (*C. arctata* × *C. castanea*)

**Carex castanea × C. debilis**

Caespitose perennial. **Fertile culms** 22–34 cm tall, with reddish bladeless sheaths at the base, these becoming filamentous with age. **Leaves** 2–5 per fertile culm, mostly in the basal third, the blades 1–8 cm long, 1.5–2.5 mm wide, pubescent with hairs 0.1–0.6 mm long on both surfaces; sheaths 3–8 cm long, pubescent with hairs 0.1–0.4 mm long, the inner band brownish-translucent, sometimes with minute reddish dots upwardly; ligule of uppermost fertile culm leaf rounded or triangular, 2.5–4 mm long, 0.5–0.8 mm wide, brownish-hyaline usually with minute red dots and a pubescent margin. **Pseudoculms** 30–45 cm long including blades 1–40 cm long, 1.5–2.5 mm wide, with sheaths to 10 cm long, ligules 3–5 mm long, as in fertile culms. **Infructescence** 12–20 cm long; spikes 3–4, peduncled, the lower peduncles 5.2–10.1 cm long; **pistillate spikes** 2–3, 23–35 mm long, with 12–21 flowers; lowermost bract with blade 6–11 cm long, 1–1.3 mm wide, sheath 30–40 mm long, the upper bracts much reduced; **staminate spike** solitary, terminal, 20–27 mm long, ca. 20–30-flowered. Lower **pistillate scales** whitish-brown or pale brown centrally with whitish-hyaline margins, ovate, acute, 2.5–3 mm long, 1.2–1.4 mm wide, 0.5–0.8 mm wide 0.5 mm from tip, more or less pubescent on the margins. Lower **staminate scales** pale brown centrally with broad white hyaline margins, oblong, rounded at the tip, 4.2–4.5 mm long, 1.2–1.6 mm wide, 0.6–0.8 mm wide 0.5 mm from tip, pubescent on the margins. **Perigynia** ascending, sessile or with a stalk to 0.1 mm long, brown when mature, often with obscure reddish dots and flecks, especially basally, glabrous, 4.5–4.9 mm long, 1–1.4 mm wide, with two prominent lateral veins and 3–5 less pronounced veins, the body ovate tapering to an obscurely bidentate beak 0.9–1.3(1.5) mm long with teeth 0.1–0.2 mm long. **Achenes** rarely developing, pale brown with lighter brown edges, trigonous, obpyriform and slightly inflated above the stalk, the

body 1.3–1.5 mm long, 0.7–1 mm wide, the basal stalk 0.2–0.3 mm. **Styles** indurate in lower third, brittle and shrivelled above, straight above achene; stigmas 3. **Anthers** 3, 0.9–1.2 mm long, not fully developed, nor exserted. Pollen mostly not developed or malformed.

MATERIAL EXAMINED: **ONTARIO**: Timiskaming District: Bayly Twp.; wooded east shore of Lower Wendigo Lake, 47°52′00″N.L., 79°41′19″W.L., Map 31 M/13 983024, 11 August 1991, *V. R. Catling & P. M. Catling 91–224* (DAO, MICH).

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# DR. THOMAS F. LUCY: EARLY BOTANIST OF THE CHEMUNG RIVER VALLEY, NEW YORK

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## ABSTRACT

Thomas Francis Lucy (1844–1906) was an eclectic medical doctor who devoted most of his life to studying the plants of the Susquehanna Valley, specifically the Chemung River Valley, Chemung County, New York. He also spent his later life collecting and exchanging specimens of North American plants. The main collection of the Flora of the Upper Susquehanna that he prepared for the Elmira Academy of Sciences is currently housed at ECH. Other specimens collected by Lucy are located at BH-CU, NYS, NY, F, US, and MIN. After his death, many of his North American specimens were deposited in BUF. These are currently being curated at ECH.

Key Words: Thomas Francis Lucy, Susquehanna Valley, Chemung County, Upper Susquehanna Flora, Elmira Academy of Sciences, Elmira College Herbarium, New York; Buffalo Academy of Sciences, New York

## INTRODUCTION

This biography summarizes the life and work of Dr. Thomas F. Lucy (1844–1906, Figure 1, Table 1), who lived and collected botanical specimens in the Chemung River valley, New York, for more than 30 years (1868–1900; Clute, 1898; Smithsonian Institution Archives, Record Unit 221). Lucy's herbarium and the records of other local botanists provided the framework for Clute's (1898) *Flora of the Upper Susquehanna and Its Tributaries*. Clute's book was important during this period, for it completed a "chain of local floras extending from eastern Pennsylvania to Lake Ontario" (Clute, 1898). In the late 1890's, Lucy donated more than 1500 beautifully mounted and meticulously labeled botanical specimens to the Elmira Academy of Sciences (Kelloff et al., 1990). Today this collection forms the nucleus of the Elmira College Herbarium (ECH).

## PERSONAL LIFE AND EDUCATION

Thomas Francis Lucy was born on 7 June 1844 in Bredons Nortin Hall parish, Worcester, England. He was the son of Henry

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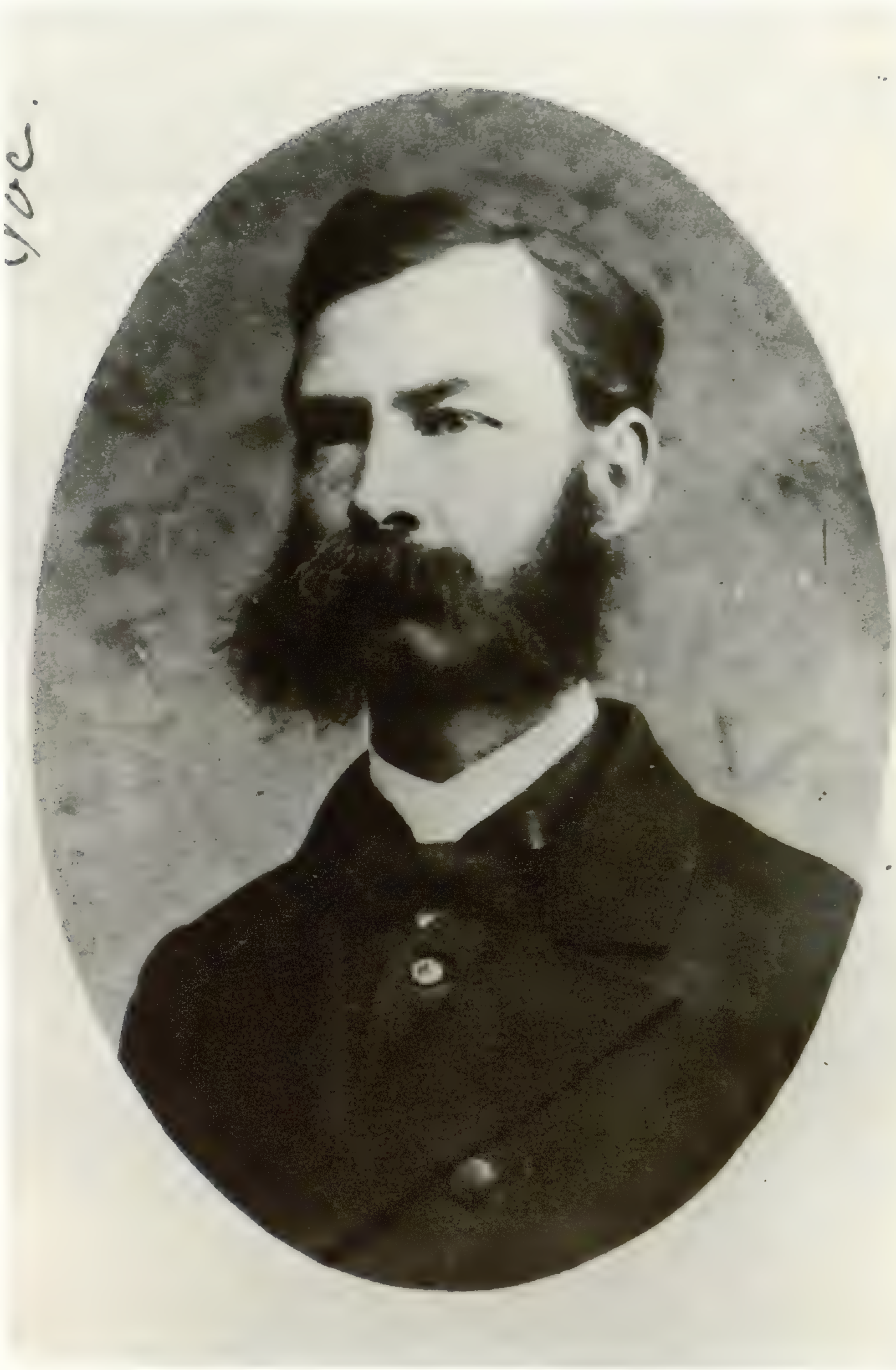

Figure 1. Photo of Dr. Thomas Francis Lucy from a postcard written ca. 1900 to his daughter Maud (Mrs. Hattie "Maud" Seaman), who donated it to the New York State Museum at Albany, NY (1938b).

Table 1. Chronology of the life of Thomas Francis Lucy M.D. (1844–1906).

| | |
|---|---|
| 1844 | Born in Worcester, England |
| 1850's | Lived in Corning, New York |
| 1865–66 | Attended Hobart College, Geneva, New York; Member Chi Phi Fraternity |
| 1868 | Naturalized Citizen of USA |
| 1870–77 | Married Josephine Searles, had two daughters; Lived in Ashland, New York |
| 1879 | First main botanical collections |
| 1881 | M.D. Eclectic Medical College of the City of New York<br>Chairman of Botany, Elmira Academy of Sciences<br>First botanical publication |
| 1880's–1900's | Collected plants for "Upper Susquehanna Flora" |
| 1882 | Elected to American Society of Microscopists |
| 1883–1900 | Lived in Elmira, New York |
| 1888 | Listed in Cassino's *International Scientist's Directory* |
| 1891 | Corresponding member Torrey Botanical Club |
| 1892–1900 | Prepared Herbarium of "Upper Susquehanna Flora" for the Elmira Academy of Sciences |
| 1895 | Listed in Cassino's *Naturalist's Directory of the United States and Canada* |
| 1898 | Publication of Clute's *Flora of the Upper Susquehanna and It's Tributaries* |
| 1899 | Advertised sale of duplicate specimens for "Flora of the Upper Susquehanna" |
| 1900 | Moved to Buffalo, New York |
| 1906 | Died in Buffalo, New York<br>Lucy's duplicate plant specimens donated to Buffalo Academy of Sciences |

Lucy, an English barrister, and Sarah Hook Lucy (Bureau of Vital Statistics—Buffalo, 1906; New York State Museum at Albany, 1938a). The Lucy family came to America in the mid-1850's, settling in Corning, New York (New York State Census, 1855). Thomas F. Lucy and his younger siblings, Ellen S. Lucy and Harry W. Lucy, lived in Corning with their mother and attended school (Federal Census Records, 1860). Henry Lucy, apparently unable to find work in the Corning area, became a merchant in New York City (New York State Census Records, 1865).

In 1865, at age 21, Thomas F. Lucy enrolled at Hobart College, Geneva, New York (Catalogue of Hobart College, 1865–66) and was initiated into the Upsilon Chapter of the "Secret Order of Chi Phi" on March 14 (Chi Phi Centennial Memorial Volume,

1924; Hobart College, 1865, 1867; Robson, 1977). During the late 1800's it appears to have been the custom for college authorities to grant charters to secret societies, wherever established. The Alpha Omega Fraternity of Hobart College was established in 1866. Lucy is listed as President and provider of this society (Hobart College, 1866). The objective and number of society members are unknown. The Alpha Omega Fraternity dropped into obscurity as quickly as it was established. During his sophomore year at Hobart, Lucy was the class historian (Hobart College, 1866). It was noted in the Catalogue of Hobart College (1866–67) that Lucy was not in residence when the Catalogue went to press. According to the President's Report (1909–1911), Lucy was listed as being a "non-grad."

Sometime prior to September 1868, Lucy submitted his application and petition for naturalization to the Steuben County Courthouse, Bath, New York. On 28 September 1868, as witnessed by Frank Brown and George Graves of Corning, New York, Lucy became a citizen of the United States (pers. comm.—Marianne Springer, County Clerk's Office, Bath, New York).

Sometime after 1870, Lucy married Josephine Searles, born 1849 (Chemung County Historical Society, 1976) and daughter of Alfred Searles, farmer and mill-wright (Child, 1868) and Sarah Baker Searles of Pennsylvania (Bureau of Vital Statistics—Elmira, 1890). Josephine was a school teacher in Ashland, New York (Federal Census Records, 1870). They lived on the Searles farm in Ashland and had two daughters, Anna May, born 1876, and Hattie Maud, born November 1877 (Federal Census Records, 1880a, 1880b, 1900a).

In 1881 Lucy received his Doctor of Medicine degree from the Eclectic Medical College of New York City (Barnhart, 1965). According to the Eclectic Medical College of the City of New York Annual Announcement (1867), the goal of "eclecticism [as practiced at the college] aim[ed] to enlarge and improve the most important portion of practical medicine, . . . in exploring our indigenous medical botany, and obtaining the medicinal principles isolated from each plant, so as to administer in the smallest dose and most agreeable form." In addition, ". . . no medical treatment should be allowed that permanently impairs the vital powers." The candidates were required "to have attained the age of 21" and be "of good moral character." Requirements for graduation included the stipulation that candidates must have studied med-

icine with a "respectable practitioner" for 2–4 years and must have attended several "full courses of lectures" at an accredited college. Since it was required for the candidate to attend the last lectures at the Eclectic Medical College, Lucy probably resided in New York City during this time. The Eclectic Medical College of the City of New York closed its doors in 1913 due to an inability to meet American Medical Association supported guidelines (Letter from W. C. Black, Archivist, Lloyd Library and Museum, to L. Kass and C. Kelloff, 4 August 1992).

We believe that Lucy's interest in botany was reinforced by his education in Eclectic Medicine. Although Lucy is listed as a physician in the 1887 Elmira City Directory and the 1901 Buffalo City Directory, we were not able to find that he had any affiliation with local hospitals or local or regional Medical Associations. If he was a practicing physician he may have initially collected plants for use in treating his patients. It appears, however, considering his affiliations with scientific societies, his interests in medicinal plants led to his life's work of studying the natural history of the plants of Chemung County and surrounding regions. He may have been able to devote time to his interest in botany due to the financial support provided by his wife.

In August 1882, the American Society of Microscopists held their fifth annual meeting in Elmira, New York. It was on the 15th of August that, "on recommendation of the Executive Committee," Thomas F. Lucy was "elected to membership in the Society" (Proceedings of the Amer. Society of Microscopists, 1882). Lucy was dropped from the rolls in 1889 when the society had failed to receive correspondence from him in the preceding three years.

Lucy and his family initially lived in the New York towns of Wellsburg, Lowman, and Chemung. Lucy botanized these areas, as his herbarium labels revealed (Figures 2A and B). From Lucy's (1883a, 1883b) "Notes from Chemung county, N.Y.," published in the *Bulletin of the Torrey Botanical Club,* we learned that Lucy had moved to Elmira, New York, where he subsequently developed an affiliation with the Elmira Academy of Sciences. On 14 April 1885 Josephine Lucy purchased a house for $600 at 215 Mt. Zoar Street, Elmira, from Charles and Aurelia Davis (Chemung Deeds, 1885).

Josephine Lucy died on 21 January 1890 after a long illness (Bureau of Vital Statistics—Elmira, 1890). In her Will (Chemung

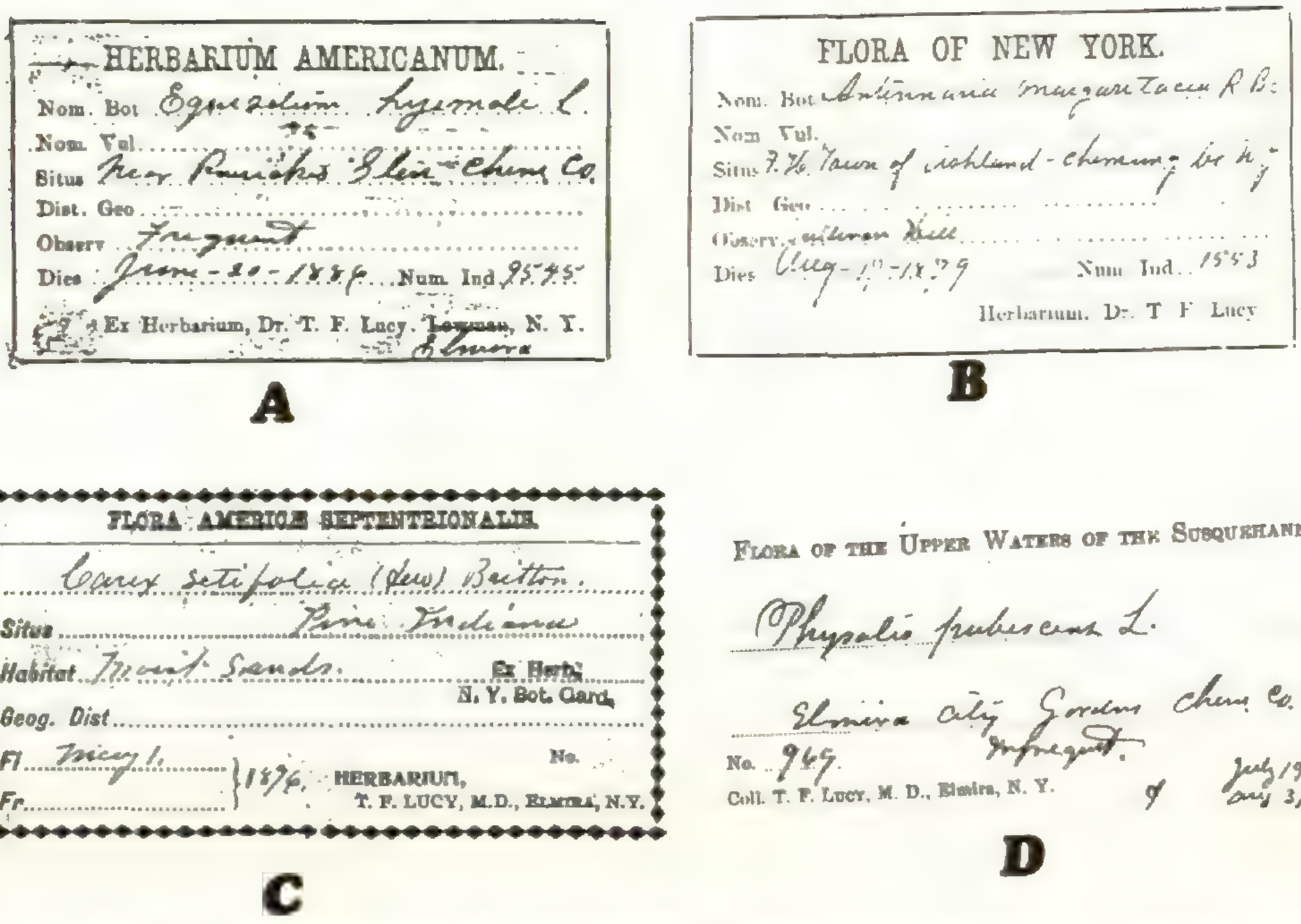


Figure 2. Examples of the various types of herbarium labels used by Thomas Francis Lucy. These labels are less documented compared with the labels Lucy prepared for the Elmira Academy of Sciences "Upper Susquehanna Flora (Kelloff et al. 1990)." A. and B. Unmounted labels from Lucy's collection given to BUF after his death in 1906. C. Label from herbarium specimen at US obtained in an exchange with NY. D. Label from herbarium specimen at CU in the herbarium of Stewart H. Burnham.

Deeds, 1889), Josephine left "all of [her] estate real and personal" to her two daughters "May Lucy" [14 yr.] and "Maud Lucy" [12 yr.]. To her husband she left "all monies accruing from [her] shares in the . . . Chemung Valley Mutual Loan Association over and above sufficient to pay all [her] obligation hereto. . . ." and "one complete set of the Encyclopaedia Britanicai [sic] to complete [her] last wishes as a gift intended for him."

After Josephine's death, Lucy married Martha "Emma" Shirey, and remained at Mt. Zoar Street with his two daughters, Anna May and Hattie M. [Maud] (Chemung County Census Records, 1892). Emma was born December 1862 (Federal Census Records, 1900a) in Clearfield, PA (New York State Museum at Albany, 1938a). By 1896, Emma's brother, Wallace Shirey, a Linotype operator for the Gazette office in Elmira, also boarded at Mt. Zoar Street (Hanford, 1896). The Elmira City Directory for 1896 (Hanford, 1896) does not list Anna May as a resident at Mt. Zoar. According to the Indenture (Bill of Sale) for the Mt. Zoar property

(Chemung Deeds, vol. 102, p. 432), Anna May was married to a Mr. Smith (date unknown) and lived in New York City. In a postcard written ca. 1900 (New York State Museum at Albany, 1938b), Lucy expressed his concerns to Maud about his older daughter: "wrote to May at Buff[alo] [but have] not heard anything from her since she wrote before Xmas." He asked Maud how she liked the photo of him (Figure 1), which was printed on the card, and sent his love to the "babes."

The Indenture (Chemung Deeds, 1899) also revealed that Maud had married a Mr. Seaman and was living in Elmira. The Federal Census Records (1900b) revealed that Maud was married to Willice M. Seaman, lived at 507 Baldwin, Elmira, and had a daughter, Irene D., born May 1900. They later moved to 153-½ Steuben Street, Utica, New York, where Willice worked for Martin & Seaman (Utica City Directory, 1904; Anon., 1906). From the file to which the above mentioned postcard is attached, we learned that in 1938, Mrs. Hattie "Maud" Seaman, the donor of this postcard, resided in Little Falls, New Jersey.

Lucy purchased the house on Mt. Zoar Street from his two daughters, Anna May Smith and Hattie M. Seaman, on 27 May 1899 for the sum of $1500.00 (Chemung Deeds, 1899). In a letter to New York State Botanist Charles Peck (1833–1917), 6 October 1900, Lucy stated that he had recently moved to Buffalo, New York (New York State Museum at Albany, 1900). He may have made this move to be closer to his daughter May and his wife's sister Mrs. Lewis C. Lanich and her brother Wallace, who boarded with Lanich (Federal Census Records, 1900a). Lucy died in Buffalo on 29 October 1906 of Bright's Disease (Bureau of Vital Statistics—Buffalo, 1906). Emma is believed to have died only a few months later in February 1907 (New York State Museum at Albany, 1938a).

## EARLY INTERESTS IN NATURAL SCIENCES

Thomas F. Lucy had a broad interest in the natural sciences. In 1878, he wrote to Spencer F. Baird (1823–1887), Secretary Smithsonian Institution, Washington, D.C. requesting information and an assortment of publications. Baird was pleased to write back (Smithsonian Institution Archives, Record Unit 33) that he was able to "supply [Lucy] with a copy of Morris' [1862] Synopsis

of Lepidoptera, as requested." Lucy had also offered to collect birds and their eggs for the National Museum, but Baird stated that the Museum would only be interested in "specimens of the rarer species." In this same correspondence, Baird referred Lucy to J. M. Emerton of Salem, Mass., as an authority on spiders. In other letters to Baird, Lucy requested copies of H. Loew (1862, 1864, 1873) and R. Osten Sacken's (1869) *Monographs of the Diptera of North America,* parts 1–4; *Classification of the Coleoptera of North America* (Le Conte, 1862, 1873), and also requested "M.O. Vol. 3$^{d}$ 1862" (Smithsonian Institution Archives, Record Unit 28). Lucy also requested the Toner lectures I–VII (Woodward, 1873; Brown-Sequard, 1877; DaCosta, 1874; Wood, 1875; Keen, 1876; Adams, 1877; Shakespeare, 1879), which were given in Washington, D.C. on medical subjects.

At Elmira College we located a large 10¾ × 16¼ × 1¾ inch leather-bound book in which Lucy kept notes on his readings and research in natural science. This notebook is currently housed in the Elmira College Herbarium (ECH) and will be deposited in the Elmira College Archives. Among his first entries were tables, notes and descriptions of "Coleoptera" [beetles] "common to the Eastern and Western Continents" as well as those "peculiar to America, concentrating on Russian America" and species found in Oregon and California. In addition to beetles, Lucy kept notes on fishes from California, Rocky Mountains and the Oregon Territory as reported by "Hayden's Survey of Montana and adjacent Territories 1891." Other "orders" of organisms he listed from Hayden's survey are "Odonata" [dragonflies], "Hemiptera" [true bugs], "Lepidoptera" [butterflies and moths], "Orthoptera" [grasshoppers] and "Plants."

Lucy listed 384 plants including their localities and abundance from "No. 3 Catalogue of Plants collected in Washington Territory Vol. 12 Part 2$^{d}$. Plants Collected from the Summit of the Cascade Mts. Eastward to the upper Columbia River, and Northward to the 49$^{th}$ Degree of Latitude between July & Sept. 1853 [No author cited]."

In one 38-page section of his notebook Lucy listed a "Flora New York State," beginning with "Order I Ranunculaceae" and ending with "Order 120 Lycopodiaceae." Using red ink he listed genera and species followed in black ink by counties where the plants should be found and often a date when he apparently located them.

i.e., "Coptis trifolia [in red ink] Salisb. Cohocton Stub.
1872
[Steuben] Co. Aug. 3. Bogs. Chemung Co. [underlined in red] Lowmans Swamp."

Lucy made notes on "the Geographical Distribution of British Mosses" and "Outlines of British Fungology" by the Rev. N. J. Berkley; an "Introductory Essay to the Flora of Tasmania" by J. D. Hooker, and various plant classification systems including an extensive listing of "Bentham and Hooker's Classification. Reg.[num] Veg.[etabilia]." Tables of fossil animals and plants are listed throughout the notebook. It is obvious from his notes and letters to Dr. Lucy was interested in all aspects of natural history.

## LUCY'S BOTANICAL INTERESTS

Although Lucy's initial interest in natural history was entomological, the first record of his interest in botany was published in 1881, the year he graduated from medical school, as a note in the *Bulletin of the Torrey Botanical Club* (Lucy, 1881). Here, he commented on finding a single specimen of "Cacalia atriplicifolia L. at the side of the railroad at Wellesburg [sic]" in 1874. Having not seen the plant again, Lucy wondered if the seed had been dropped by a passing train. Lucy reported (1891) that his first main botanical collections were made in 1879. Between 1895 and 1898 Lucy sent 266 of his specimens to the University of Minnesota Herbarium (MIN, letter from B. G. Ownbey to C. Long, 4 Nov. 1986). Clute (1898) reported that Lucy had probably been botanizing since ca. 1868. From Lucy's notes (Lucy 1883a) and herbarium labels (Figure 2) we know that he also made collections in the New York counties of Livingston and Steuben. But Lucy concentrated his collecting in the small County of Chemung, New York (Lucy, 1882, 1883b, 1891; Millspaugh, 1887). Most of the specimens reported by Clute (1898) for Chemung County were collected by Lucy. His herbarium labels indicate that Lucy was also interested in plants of North America (Figure 2A and C).

In a 25 June 1890 letter to the specialist in grasses George Vasey (1822–1893); see Ewan, 1969, and (Smithsonian Institution Archives, Record Unit 220), Lucy thanked Vasey for sending him the No. 1 Contributions of the United States National Herbarium (Vasey and Rose, 1890a, 1890b). He also stated that he was "particularly interested in the Solidagos and Asters" and wanted spe-

cies from the southern states for comparison in order to complete his herbarium. He was willing to exchange specimens with any southern botanist. In the same letter, Lucy commented that Millspaugh said he, Lucy, had a finer collection than Cornell University. He also told Vasey that his collection was filled with northwestern species and that Dickenson [whom we believe to be J. Dixon] & [D.] Drake of Portland, Oregon, "say I send them the best specimens they receive."

Lucy was listed in the *Bulletin of the Torrey Botanical Club* (1891) as a corresponding member, was listed in the *Naturalist's Directory of the United States and Canada* (Cassino, 1895) and the *International Scientist's Directory* (Cassino, 1888).

## THE ELMIRA ACADEMY OF SCIENCES— UPPER SUSQUEHANNA FLORA

Lucy's botanical career advanced after he moved to Elmira and became affiliated with the Elmira Academy of Sciences. This society was established in 1861 for the "pursuit of astronomical and scientific studies" (Elmira Academy of Sciences, 1881) and was housed in the Observatory opposite the Elmira Female College (name changed to Elmira College in 1890—Barber, 1955). The Observatory was acquired by the college in 1881 (Barber, 1955; Kelloff et al., 1990). Lucy is listed as Chairman of the Elmira Academy of Sciences' Section of Botany (Elmira Academy of Sciences, 1881, 1897) and a member of the Council of Administration for the year 1886 (Elmira Academy of Sciences, 1881).

As reported by Clute (1898) in the preface to the *Flora of the Upper Susquehanna,* "Dr. Lucy has also presented to the Elmira Academy of Sciences a nearly complete collection of the plants of our region." This collection is currently housed in the Elmira College Herbarium (ECH, Kelloff et al., 1990).

*Flora of the Upper Susquehanna* was part of a "general plan for an extended study of the flora of the headwaters of the Susquehanna river" (Clute, 1898). Based in Binghamton, Broome County, New York, Clute (1869–1950) found that very little had been published on the flora of this region. The collections and notes of local botanists provided the needed information for this project. As described in Clute's (1898) preface these botanists were "Mr. Frederick V[ernon]. Coville [1867–1937], Botanist of the

United States Department of Agriculture, [who] made a very careful examination of the botany of central Chenango county. Dr. C[harles]. F[rederick]. Millspaugh [1854–1923], now curator [appointed 1894] of the Field Columbian Museum, Chicago, made many observations upon the flora in the vicinity of Binghamton and Waverly during ten years' practice of medicine [1881–1891] in these places. It was in this region that most of the plants figured in his "American Medicinal Plants" [1884] were studied and depicted [in 1920, Millspaugh published *The Bahama Flora* with N. L. Britton (1854–1923), curator at NY]. Mr. David F[letcher]. Hoy [1863–1930], Registrar of Cornell University, has collected several seasons in the Susquehanna valley in Delaware county. Dr. Thomas Francis Lucy [1844–1906] has devoted much of his time to the botany of the Chemung valley for the past thirty years. Mr. James A[nsel]. Graves [1828–1909], has botanized extensively in the lower Chemung valley, and for the past twenty years has made careful observations on the flora in the vicinity of Susquehanna borough, his home. Prof. Frank E[rnest]. Fenno [d. 1920], in the past three years has been indefatigable in investigating the botany of Barton, Apalachin and intermediate points. Mr. W[illiam]. C[lay]. Barbour (1877–1933), has contributed many notes on the plants of Sayre, Athens and Waverly, and Miss S. A. Brown, has favored us with a very complete list of plants with notes from the vicinity of Unadilla Forks. The author's knowledge of the flora was acquired during a ten years' residence at Binghamton, in which time the greater part of the region came under his observation (Clute, 1898; Ewan, 1969; Barnhart, 1965; Stafleu and Cowan, 1979)."

In a letter to New York State Botanist Charles Peck (New York State Museum at Albany, 1900), Lucy reported: "I have just completed my work for the Elmira Academy of Sciences, which I commenced in 1892." It was during this time that Lucy began to advertise the sale of his duplicates for the "Flora of the Upper Susquehanna . . . at the rate of Five Dollars per 100 species," or priced according to their rarity, in a flyer dated December 1899 (Smithsonian Institution Archives, Record Unit 221). This flyer sent to the Smithsonian, stated that "lists of species per Patterson's [1892] or Heller's [1898] check-list could be purchased." In response to receiving Lucy's flyer, F. V. Coville (1867–1937) Botanist, United States Department of Agriculture, asked J. N. Rose (1862–1928), Assistant Curator, Department of Botany, Smith-

sonian Institution, his thoughts on this flyer. Rose replied to Coville on 25 January 1900 (Smithsonian Institution Archives, Record Unit 221), "Mr. Pollard (1872–1945) [Curator of Plants, Department of Botany, Smithsonian Institution (1895–1903)] thinks that Dr. Lucy's collection from the Susquehanna would be of undoubted value," although the National Herbarium must already "have abundant material" from this area. Coville again asked Rose what he recommended. Rose then replied "simply make a selection of the most desirable of these plants." On the back of the memorandum, C. L. P[ollard] commented to Rose, "this set would be of undoubted value [since] we have very little from the Chemung Valley." It was noted on this same memorandum that a letter was sent to Dr. Lucy on 6 February 1900. Lucy replied to Coville on 12 February 1900: "Herewith I send you a list of my Susq. Flora species, numbered according to Patterson's check-list for all those I can now supply. Please check those which you may desire and return same." We found no further correspondence in the files. According to the National Museum of Natural History Registrar's Office, the Smithsonian never purchased nor received directly Lucy's collections from the Susquehanna Flora. However, in that same year Lucy donated 100 specimens from the Susquehanna Valley, New York, to the newly established herbarium of the New York Botanical Garden (*Journal of the New York Botanical Garden,* 1900). Additionally, another 200 specimens from western New York were sent on exchange to the herbarium of the New York Botanical Garden (*Bulletin of the New York Botanical Garden,* 1900). The Smithsonian eventually acquired some of Lucy's specimens in an exchange with the herbarium of the New York Botanical Garden (Figure 2C). In 1990, at the New York State Museum herbarium (NYS), we located a number of Lucy specimens collected during the 1880's. Some of these specimens were obtained in exchange with NY. The curators at NYS informed us that they do not have the acquisition records or details of their holdings of Lucy's specimens.

Dr. Lucy's specimens have been reported by Chaudhri et al. (1972) as being located at F, MIN, NY, NYS, and BUF. We have also located specimens at US, on exchange with NY as noted above, and at BH-CU (Figure 2D) probably in exchange with Stewart Burnham (1870–1943), Assistant Curator at CU, whose specimens are in the Lucy collection at EC.

## LUCY IN BUFFALO, NEW YORK

In a letter to Charles Peck of 6 Oct 1900, sent from Niagara Street, Buffalo, N.Y., Lucy expressed an interest in getting a position that he had learned of from Miss Sletron of the Buffalo Academy of Sciences. The position was on the State Botanical Survey. We do not know whether Dr. Lucy received this appointment.

Lucy was also interested in *Salix* of northwestern United States. In March 1904 he wrote to C. V. Piper (1867–1926) (Office of the Agrostologist), requesting specimens of *Salix* from that region (Hunt Institute for Botanical Documentation, 1904a). Lucy received a reply from Carlton R. Ball (1873–1958), Assistant Agrostologist, informing him that he would be "glad to negotiate exchange for material from the Southern and Eastern United States" (Hunt Institute for Botanical Documentation, 1904b). Lucy replied to Ball's letter on 3 May 1904 thanking him for his information (Hunt Institute for Botanical Documentation, 1904c). In this same response he informed Ball that he now had "7583 sheets" of North American species and that he would be glad to send some of them in exchange, if he received a list of required species listed by Patterson's [1892] or Heller's [1898] check-list numbers.

## CURRENT STATUS OF LUCY'S PERSONAL HERBARIUM

After Lucy's death in 1906, his botanical collection, still in newspapers, was donated to the Buffalo Academy of Sciences by Emma's sister, Mrs. L. C. Lanich (New York State Museum at Albany, 1938a; letter from R. Zander to C. Long and L. Kass, 21 January 1986).

In 1986, when it was shown to us, the collection was in the original condition; except that some specimens having complete label information had been filed in the BUF collection. Until that time BUF curators had no way to identify most of the specimens by the numbers that were written on the newspapers. However, by using the Lucy specimens at Elmira, we determined that the numbers were either Patterson or Heller check-list numbers (Kelloff et al., 1990). Apparently the donated specimens had not been accompanied by Lucy's catalogues or field notebooks. In 1988 arrangements were made for these duplicate specimens to be cur-

ated. The Lucy duplicate collection from BUF is currently being compared with the original Lucy collection at ECH. ECH will provide full labels and a complete set of duplicates to be sent back to BUF.

## CONCLUSIONS

Although Thomas F. Lucy pursued a degree in medicine, he apparently did not practice this profession. Prior to his pursuit of medicine, he seems to have been widely interested in natural history, concentrating initially on insects and birds and subsequently on invertebrates, vertebrates and then plants. The year he graduated from medical school his interests in botany seemed to swell and he became the Chairman of Botany for the Elmira Academy of Sciences. It appears that he had time to pursue his botanical interests due to the financial support provided by his wife. Because he prepared a meticulously labeled plant collection for the Elmira Academy of Sciences and kept extensive notes on his research and readings, it is difficult to believe that he did not have a carefully kept field notebook or catalogue of his collections. Unfortunately, we have not located such a book and believe that it may have been lost prior to his sister-in-law's donating his private herbarium to the Buffalo Academy of Sciences. It pleases us to have been able to uncover so much information on Dr. Lucy and his contributions to the flora of New York State. This in spite of the amount of time that has passed since he began his studies of the flora of one small county.

## ACKNOWLEDGMENTS

We thank the following people for their help and encouragement during this project. Dr. Steve Clemants for locating the photograph of Dr. Lucy at the New York State Museum, Albany; Robert Dirig for continued encouragement and professional assistance; Richard Hurley for locating information on Chemung County; Anita Jacobs for locating Dr. Lucy's obituaries in Buffalo; Anita Karg for bringing to our attention the Carlton Ball Letters at the Hunt Institute for Botanical Documentation; Jan Kather for preparing Dr. Lucy's photograph; Dr. Malcom Marsden for ms. proofreading; Dr. Bryan Reddick for making available financial support from Elmira College; and Dr. Richard Zander for help with the Lucy Collection at BUF.

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# DISCOVERY OF *SUBULARIA AQUATICA* L. IN COLORADO AND THE EXTENSION OF ITS RANGE

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## ABSTRACT

A new record for the vascular flora of Colorado is reported. *Subularia aquatica* L. was found growing on a muddy, subalpine lake bottom in north-central Colorado during the field season of 1992. This extends its previously known range in the Southern Rocky Mountains by approximately 220 miles (354 km) to the east from the Utah localities and 270–280 miles (435–450 km) southeastward from its Wyoming localities.

Key Words: *Subularia aquatica* L., Colorado, vascular flora, range extension

Field work during the summer of 1992 has added a new record to the vascular flora of Colorado. Treatments by Coulter (1885), Rydberg (1917), Fernald (1950), Gleason (1952), Harrington (1954), Gleason and Cronquist (1963), Mulligan and Calder (1964), Dorn (1988), Weber (1976, 1987, 1990), and Weber and Wittman (1992), do not indicate that *Subularia aquatica* L. occurs in Colorado.

*Subularia aquatica* L. is a dwarf, aquatic or littoral mustard, in which the flowers are either self-pollinating or when submerged are cleistogamous. Subula from the Latin refers to the awl-shaped leaves which lend to the common name of awlwort. Often found in clear, cold water lakes at higher elevations (Mulligan and Calder, 1964), the plants grow on muddy bottoms of lake margins (Gleason, 1952).

The discovery of *S. aquatica* in Colorado was made in the Neota Wilderness Area, Larimer County, (R75W, T7N, Sec. 33), in a small unnamed lake at an elevation of 10,354 ft. Mulligan and Calder (1964) report that *S. aquatica* is often found growing in conjunction with other plants which have similar awl or grass-like leaves. They give *Eleocharis acicularis* (L.) R. & S. and similar species of *Limosella* as examples. The Colorado specimens were found growing abundantly on the muddy lake bottom in association with *Isoetes bolanderi* Engelmann another abundant species there.

The discovery of *S. aquatica* L. in Colorado significantly expands its previously known range in the Southern Rocky Mountains. Widely distributed across the northern hemisphere from

Greenland, Iceland, northern Europe to the Urals, then disjunct to Kamchatka, and then extending from Alaska to Newfoundland, its furthest distribution southward in North America is into California, Utah, and Wyoming (Mulligan and Calder, 1964).

The closest collections to the Colorado location are from Mirror Lake, Duchesne Co., Utah and New Fork Lakes, Sublette Co., Dinwoody Creek, Fremont Co., and Yellowstone Lake, Yellowstone National Park, all in Wyoming (Mulligan and Calder, 1964). This discovery of *S. aquatica* L. in Colorado extends its range eastward from Utah by approximately 220 miles (354 km) and its range southeastward from the Wyoming localities by approximately 270–280 miles (435–450 km).

Voucher specimens are being deposited at the University of Northern Colorado Herbarium at Greeley (GREE), the University of Colorado Herbarium at Boulder (COLO), and the Rocky Mountain Herbarium at Laramie (RM).

Special thanks are given to Dan Bach and John Moore for their assistance.

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# FIRE AND *CUSCUTA GLOMERATA* CHOISY IN OHIO: A CONNECTION?

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## ABSTRACT

*Cuscuta glomerata* Choisy is a distinctive species largely confined to the central and midwestern prairie region. It was noted as extirpated in Ohio in 1988 (the last collection dating from 1933). Since 1989 five stations for the species in Ohio have been located. All are associated with prairie remnants which have, in recent years, been subjected to regular controlled burning. It is suggested that fire is essential to rupture the seed coat and stimulate germination.

Key Words: *Cuscuta glomerata,* Ohio, prairie, fire

*Cuscuta glomerata* Choisy (Cuscutaceae), colloquially known as Rope-dodder (Gleason and Cronquist, 1991), is a distinctive species in a genus noted for difficulty in species separation (Austin, 1979). While some species are partly autophytic, many species lack chlorophyll and appear to be entirely parasitic. Rope-dodder is easily identified by its dense, elongate, continuous flower clusters which, when in flower, resemble a thick orange-colored pipe-cleaner twining among the vegetation (Figure 1). Other characters which separate *C. glomerata* from other eastern North American species are its capitate stigmas, distinct sepals, and sessile flowers subtended by several loosely ascending bracts with recurved tips. Rope-dodder exhibits a tendency to parasitize species of Asteraceae, such as *Ambrosia, Aster, Helenium, Helianthus, Liatris, Silphium, Solidago* and *Vernonia* (Yuncker, 1965). Members of these genera are commonly found in prairies, and the range of *C. glomerata* is largely confined to the central and midwestern prairie region (Fernald, 1950).

Fire is known to play an important role in prairie ecosystems by stimulating and maintaining populations of certain prairie species (Anderson, 1982). Historical accounts by early pioneers settling mid-western and central prairie regions report on the ferocity and frequency of these blazes (Brown, 1883). As prairies diminished in size and became increasingly fragmented with the advance of civilization, fire suppression became the norm and thus prairie fires were virtually eliminated (Curtis, 1959). In recent years natural-areas managers have begun to use fire as a tool for the management of prairie communities. In 1983, the Ohio De-

Figure 1. *Cuscuta glomerata* parasitizing *Solidago canadensis* in Milford Center Prairie, Union County, Ohio.

partment of Natural Resources (ODNR) began to experiment with controlled burning on state-owned prairie areas. Since that time ODNR's controlled burning activities have become a vital part of the state's natural areas management program. In the springs

Table 1. Correlation between burning history and discovery of Ohio *Cuscuta glomerata* populations.

| County | Year Discovered | Fire History |
|---|---|---|
| Madison | 1920 | ? |
| Pickaway | 1930 | ? |
| Madison | 1933 | ? |
| Logan | 1989 | 1984, 1985, 1986, 1987, 1988, 1989 |
| Logan | 1989 | * |
| Wyandot | 1990 | * |
| Union | 1991 | 1987, 1988, 1989, 1990, 1991 |
| Wyandot | 1992 | 1992 |

* Discussions with landowners revealed that these sites have been burned several times in the last decade, but they were unsure of which years.

of 1991 and 1992, ODNR conducted 17 prescribed burns on 10 prairies.

In Ohio, most of the prairie areas which existed prior to European settlement have been eliminated; only small, isolated fragments remain (Cusick and Troutman, 1978). Since natural forces such as fire no longer maintain these areas, prairie remnants in many cases have been further reduced by the invasion of non-native and woody species. This successional process and destruction of habitat has resulted in several prairie species being listed as extirpated in Ohio, such as *Besseya bullii* (Eaton) Rydb. (Kittentails), *Perideridia americana* (Nutt.) Reichb. (Perideridia), *Viola pedatifida* G. Don (Prairie Violet), *Dalea purpurea* Vent. (Purple Prairie-clover), and *Oenothera triloba* Nutt. (Stemless Evening-primrose). Other prairie plants are listed as endangered or threatened, including *Silphium laciniatum* L. (Compass-plant), *Gentiana puberulenta* J. Pringle (Prairie Gentian), *Valeriana ciliata* T. & G. (Prairie Valerian), *Baptisia lactea* (Raf.) Thieret (Prairie False Indigo), *Sporobolus heterolepis* A. Gray (Prairie Dropseed), *Platanthera leucophaea* (Nutt.) Lindl. (Prairie Fringed Orchid), and *Cypripedium candidum* Muhl. (White Lady's-slipper) (Division of Natural Areas and Preserves, 1992). *Cuscuta glomerata* was listed as extirpated in Ohio until 1988 (Division of Natural Areas and Preserves, 1988), as the last collection was from Madison County in 1933.

On August 12, 1989, the species was rediscovered in a prairie in Logan County (Peskin, 1990). Four other populations have since been located (Table 1). The first site, known as Liberty Fen

State Nature Preserve, was acquired by ODNR in 1981. The area of the preserve where the Dodder occurs has been subjected to spring burns annually since 1984. It is unlikely that *C. glomerata* was present prior to its discovery in 1989, except possibly in a dormant state. Rope-dodder is a conspicuous, easily detected species, and botanical research has been conducted at this site annually since ODNR assumed ownership. Approximately 75 plants were parasitized by the dodder, mostly *Helianthus grosseserratus* Martens (Sawtooth Sunflower), with a few *Solidago canadensis* L. (Canada Goldenrod) affected. Associates in this area include *Solidago uliginosa* Nutt. (Bog Goldenrod), *Aster puniceus* L. (Bristly Aster), *Carex trichocarpa* Muhl. (Hairy-fruited Sedge), *Physostegia virginiana* (L.) Benth. (Obedient-plant), *Solidago riddellii* Frank. (Riddell's Goldenrod), *Carex sartwellii* Dewey. (Sartwell's Sedge), and *Pedicularis lanceolata* Michx. (Swamp Lousewort).

On September 21, 1989, *C. glomerata* was located at another site in Logan County, also a moist prairie association bordering a fen. Approximately 100 host plants were infested with Rope-dodder, all of them *Solidago canadensis.* Other plant taxa in the vicinity of the dodder included *Agalinis tenuifolia* (M. Vahl.) Raf. (Common Agalinis), *Lobelia siphilitica* L. (Great Lobelia), *Chelone glabra* L. (Turtlehead), *Solidago riddellii* and *Physostegia virginiana.*

On August 25, 1990, a third population of *C. glomerata* was discovered, at Killdeer Plains Wildlife Management Area in Wyandot County. Killdeer Plains is an 8,637-acre tract located in the former Sandusky Plains, a large wet prairie which covered much of Marion and Wyandot counties. Small prairie remnants still persist in and around the wildlife area, which is owned and managed by ODNR, Division of Wildlife (DOW). Large sections of Killdeer Plains are burned on a rotating basis, and DOW personnel indicated that the site where the Dodder grows has been burned several times in the last fifteen years. Approximately 150 plants of *Helianthus grosseserratus* were parasitized by Rope-dodder. Associate species include *Andropogon gerardi* Vitman (Big Bluestem), *Silphium terebinthinaceum* Jacq. (Prairie-dock), and *Liatris spicata* (L.) Willd. (Spiked Blazing-star).

The fourth modern population of *Cuscuta glomerata* was located on July 26, 1991, in Union County. This population occurs in the largest prairie remnant associated with the former Darby Plains, which covered ca. 385 square miles in west-central Ohio

Figure 2. Ohio distribution of *Cuscuta glomerata*. × = pre 1934. ○ = post 1988. □ = original prairie areas of central Ohio. (Adapted from unpublished map by E. N. Transeau.)

(King, 1981). This site, known as Milford Center Prairie, is a narrow strip ca. 1.3 miles long on a power transmission line right-of-way owned by Dayton Power and Light. It is managed as a prairie preserve by ODNR, Division of Natural Areas and Preserves (DNAP). A number of rare or uncommon prairie plants persist here, including *Silene regia* Sims (Royal Catchfly), *Rosa blanda* Aiton (Smooth Rose), *Solidago rigida* L. (Stiff Goldenrod), *Melica nitens* Nutt. (Three-flowered Melic), and *Lathyrus venosus* Muhl. (Wild Pea). The Rope-dodder was found on approximately 30 host plants of two species, *Helianthus grosseserratus* and *Solidago canadensis,* in an area of the prairie regularly subjected to

fire. DNAP personnel have conducted spring burns at Milford Center Prairie annually since 1987. It seems unlikely that *C. glomerata* bloomed here in recent years, as this prairie is frequently visited by botanists, and is easy to examine due to its narrow width.

A fifth population of Rope-dodder was discovered on August 16, 1992, in a roadside prairie remnant near Killdeer Plains Wildlife Management Area in Wyandot County. About 75 plants of *Helianthus grosseserratus* were infested by dodder. This prairie is drier than the other *Cuscuta glomerata* sites, and associates include *Andropogon gerardi, Veronicastrum virginicum* (L.) Farw. (Culver's Root), *Spiraea alba* Duroi (Meadowsweet), *Ratibida pinnata* (Vent.) Barnhart (Prairie Coneflower), *Pycnanthemum virginianum* (L.) Durand & B. D. Jackson (Virginia Mountainmint), *Silphium trifoliatum* L. (Whorled Rosin-weed), and *Monarda fistulosa* L. (Wild Bergamot). Many of the roadsides in this area are regularly burned in the spring by local farmers, and a check with the owner of this site revealed that it has been regularly burned in recent years, most recently in the spring of 1992.

Historical collections of *Cuscuta glomerata* in Ohio are known from three sites in two counties: Madison in 1920 and 1933, and Pickaway in 1930. No habitat information is included on the labels from these collections, but both of these counties lie within former large prairie areas (Figure 2). The Pickaway Plains area extended from three to seven miles across Pickaway County (Bradley 1835), but has been almost entirely destroyed. The Darby Plains included large areas of Madison County.

Prior to European settlement, prairies covered between 700 and 1500 square miles within the borders of present-day Ohio (Cusick and Troutman, 1978). Now, only small isolated fragments exist. Because these areas are of interest to naturalists, surviving prairie remnants are well known and studied. The absence of records of *Cuscuta glomerata* in Ohio from 1933 to 1989, despite its conspicuous appearance, utilization of common host species, and occurrence in frequently studied habitats, suggests that ecological conditions necessary for the growth of Rope-dodder were lacking during this period. At least some species in the genus *Cuscuta* have hard, impermeable seed coats which allow for an extended period of dormancy, and scarification or acid treatments have been necessary in laboratory conditions to induce germination (Tingey and Allred, 1961). It is possible that heat, such as

is generated by prairie fires, may rupture seed coats and stimulate germination. The recent records of this species correspond with the re-introduction of fire into Ohio's prairie ecosystems by natural-areas managers. Since all extant Ohio populations of *Cuscuta glomerata* have appeared in areas recently burned, it appears fire may be essential to the stimulation and growth of Rope-dodder in Ohio prairies.

Voucher specimens of *Cuscuta glomerata* collected as part of this survey have been deposited in the following herbaria: CLM, KE, MICH, MU, NY, and OS (Holmgren et al., 1990).

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# THE BIOLOGY AND TAXONOMY OF THE *PORTULACA OLERACEA* L. (PORTULACACEAE) COMPLEX IN NORTH AMERICA

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## ABSTRACT

*Portulaca oleracea* L. is a polyploid, cosmopolitan weed with a broad physiological adaptability. It is morphologically variable, grows rapidly, is self-compatible producing large numbers of seeds that have a long survivability. The variability is expressed in a series of local populations that exhibit clinal variation geographically. Data obtained from the literature on the biology of the species are compared to previous taxonomic interpretations in order to develop a more functional taxonomic treatment of this polymorphic species.

Key Words: *Portulaca oleracea*, taxonomy, species biology, cytology, seed morphology

## INTRODUCTION

*Portulaca oleracea* L., purslane, is one of the world's most aggressive weeds, having been noted as the eighth most frequent plant (Coquillant, 1951) and one of the ten most noxious weeds (Singh and Singh, 1967). It is common in cultivated fields, gardens and lawns, as well as waste areas, driveways, eroded slopes and bluffs, occurring from sea level to 2600 m (Vengris et al., 1972). It is most common in the temperate and subtropical regions, although it grows in the tropics and into the higher latitudes. Legrand (1962) reports it from 45° north latitude and 40° south latitude, while Zimmerman (1977) extends this to 51° on the American continent and 54° on the European continent. Recently this had been extended to 58° in the Canadian province of Alberta (J. G. Packer, pers. comm.).

The origin of the species is uncertain and new data and interpretations have made the accepted theories questionable. De Candolle (1886) considered it to be Old World (India) spreading into the New World. Ridley (1930) suggested that *P. oleracea* is a native of deserts or desert-borders of North Africa, and Hagerup (1932) cited the Sahara as its center of origin. Although not citing this species specifically, Geesink (1969) concluded that the ancestral lineage of the genus is in Australia. In North America this species has been considered as introduced from the Old World.

It is included in Dioscorides' first century herbal (Gunther, 1959). Gray and Trumbull (1883a) summarized the evidence for a pre-Columbian existence of purslane in North America by noting that Columbus' diary (1492) had an entry reporting purslane in Cuba. Also Nuttall in Missouri and Long in what is now Colorado, reported purslane before settlers could have transported it from the east. Gray and Trumbull (1883b) allude to a possible Viking entry, possibly from Iceland into Greenland and finally into Newfoundland. There is no current report of this species occurring in either Iceland or Greenland. Additionally, Scott (pers. corresp. 1992) reports that purslane is not currently part of the flora of Newfoundland. These data support the latitudinal limits presented above.

Byrne and McAndrews (1975) report on the finding of *P. oleracea* pollen and seeds in sediment samples of a lake in southwestern Ontario, Canada, dating from the period 1430–89 A.D., with more intensive analyses extending the range from 1350 to 1539 A.D. Their explanation of this occurrence is based on man's use of the plant. Indians living in the vicinity of the lake possibly collected plants from fields and washed them in the lake, depositing the pollen and seeds in the water. In addition to the purslane residual, maize pollen (*Zea mays*) and pollen and seeds of sunflowers (*Helianthus annuus*) were also found in the same layer of sediment. Furthermore purslane seeds have been recovered from archaeological sites in Kentucky which date back to the first millenium B.C. (Watson, 1969) and from southern Louisiana dating back 1500 years (Walker, 1936). These data indicate an indigenous development or movement of the species across the continents during prehistoric times (Chapman et al., 1974). Richard Yarnell (pers. comm. 1992) suggests that *P. oleracea* has been in North America perhaps since 7000 B.C. Further insight on the success of this species can be gained by examining the biology of *P. oleracea* reported on below from the work of several investigators.

## MATERIALS AND METHODS

Herbarium specimens were obtained from: ARIZ, ASC, ASTC, ASU, BRY, CAS, COLO, DAV, DES, DUR, F, FLAS, FSU, FWM, GH, HPC, ISC, JEPS, KANU, KS, KSC, KSP, LAF, LL, LSU, MICH, MNA, MO, MU, NLU, NMC, NO, NY, OKL, OKLA, PAUH, RSA/POM, SD, SMU/BRIT, TAES,

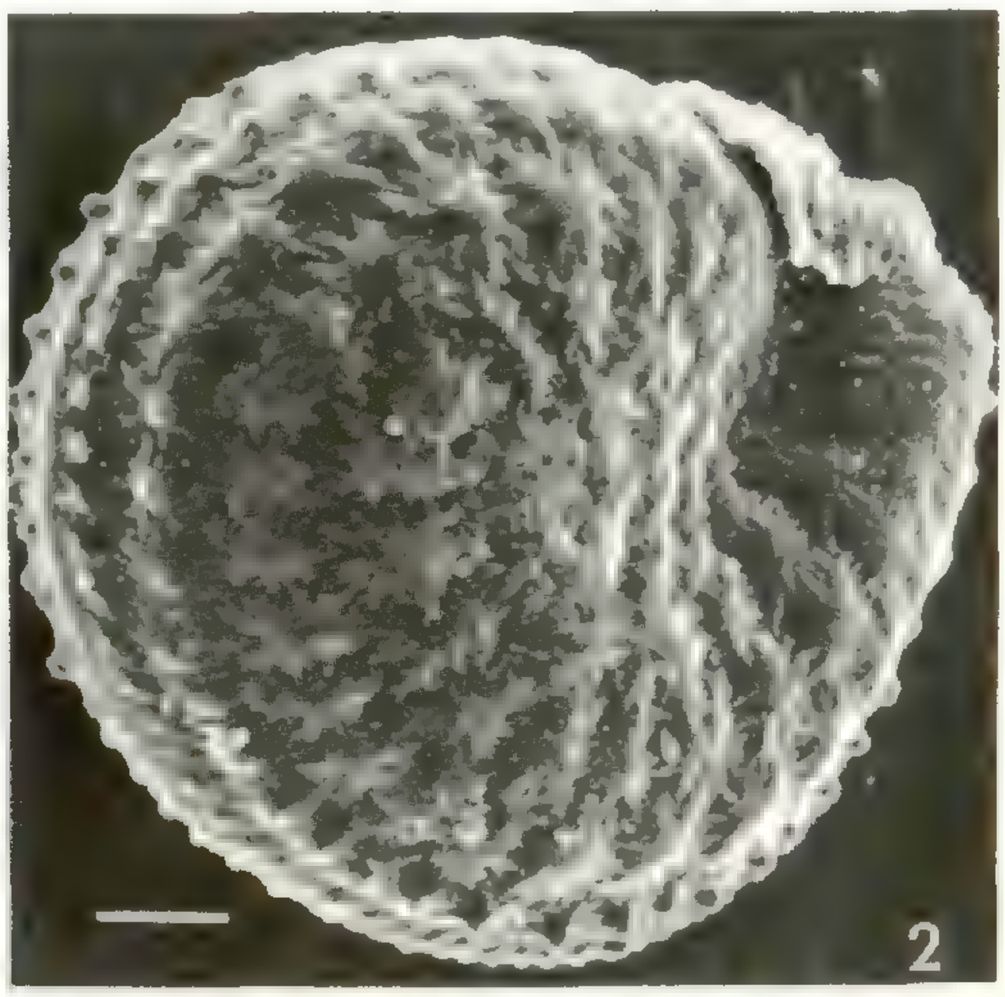
TAMU, TEX, UARK, UC, UCSB, UMC, UNCC, UNLV, UNM, US, USF, UT, UTC, UTEP, and UVST. Live specimens were collected from **California**, San Bernardino Co. (Valley between Granite and Van Winkle Mts. on Kelbaker Rd., 7 mi. N of I-40; Pass between Vontrigger Hills and Hackberry Mts., E side of Lanfair Rd., 11 mi. N of jct. Goffs Rd.); **New Mexico**, Bernalillo Co. (base of light pole, San Felipe St., Old Town, Albuquerque); **Illinois**, Jackson Co. (Lawn, Pyramids Complex, S. Rawlings St., Carbondale); **North Carolina**, Mecklenburg Co. (Garden, 5724 Doncaster Dr., Charlotte); and **South Carolina**, Beaufort Co. (Along sidewalk, Coligny Plaza, Hilton Head Island). Chromosome squashes were obtained by placing root tips in 0.1% colchicine for 1.5 hr, fixing in 3:1 alcohol-acetic acid overnight, hydrolyzing in 1 N HCl for 12 min. at 60°C, placing in Feulgen stain for four hours and squashing in dilute Aceto-carmine stain to provide cellular detail. Four plants from each site were studied. Photographs were taken using a Zeiss Axioskop equipped with Normarski differential interference contrast optics. Seed surfaces were examined and photographed, after sputter coating with gold-palladium on a Hummer V, with a Jeol JSM-35CF scanning electron microscope.

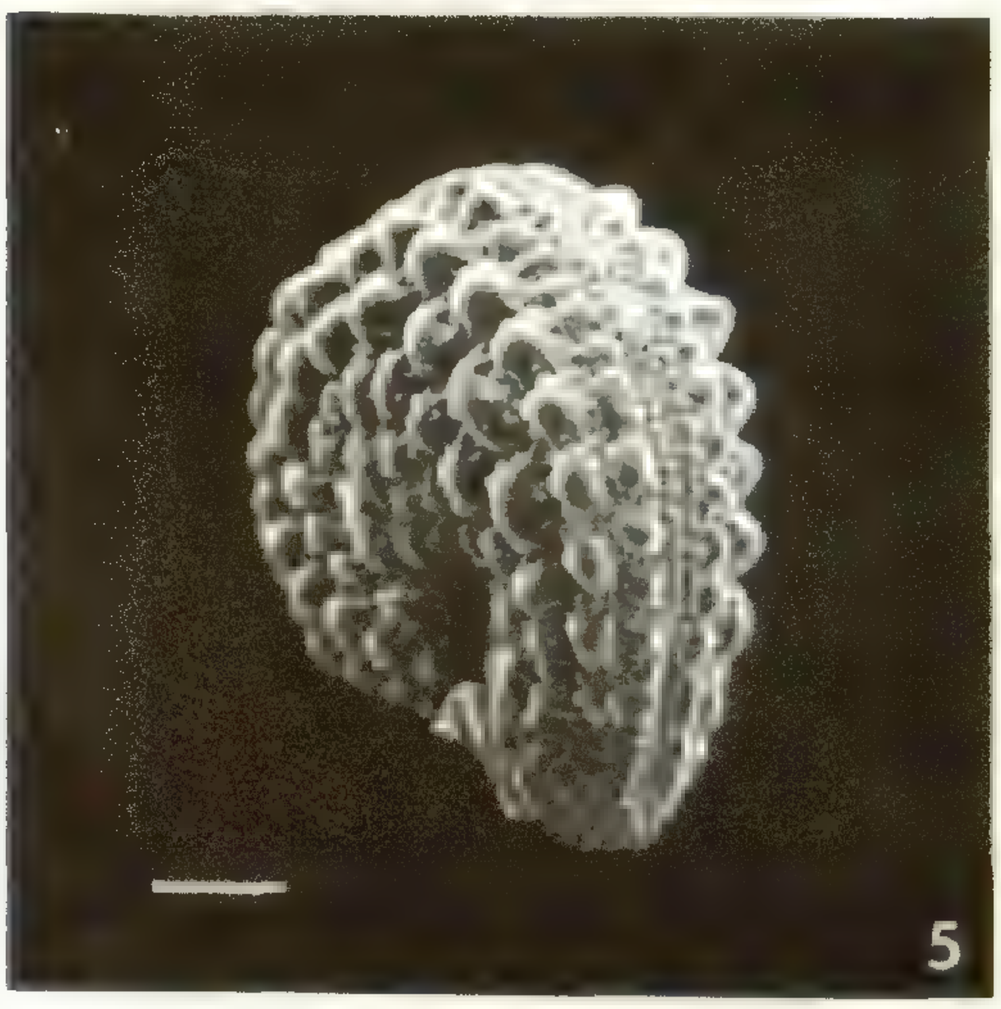
## THE SPECIES BIOLOGY OF PURSLANE

The species is mostly an annual, but may be perennial in the tropics. The leaves are alternate, subalternate or opposite, obovate to spatulate with an obtuse or truncate-emarginate apex. The leaves may range from 40 mm by 15 mm up to 60 mm by 25 mm in fertile soils. Apical verticils have 2–5 leaves, with usually 4. Axillary hairs are missing, inconspicuous, or barely visible. Flowers are in a group at the end of the stem subtended by 4 leaves. The two sepals are fused to the base of the ovary and may grow into a wing-like carina of 3–4 mm long that can cover the ripening fruit. There are (4)5(6) yellow petals ranging from 3–10 mm long by 2–8 mm wide with 6–15 (3–20) stamens. The style branches are 3–6, the capsule ranges from 4–9 mm, dehiscing at or just below the middle. Seeds are black, 0.6–1 mm, usually with granulate (Figure 1) to flat stellate (S-undulate) (Figure 2) surfaces and small tubercles along the dorsal curvature. However the seed surface can also be raised stellate (S-undulate) with tubercles on the lateral seed surfaces (Figure 3) or exhibit intermediate patterns (Legrand, 1962; Geesink, 1969; Kim, 1989).

Zimmerman (1976) reported on the growth characteristics of weediness in *P. oleracea,* in comparison with *P. pilosa* and *P. grandiflora.* Common purslane branches almost immediately after germination and therefore spreads out in its growth pattern quicker than the other two species. It produced flowers in day lengths from 4–24 hours, with a direct correlation between increased illumination and flower production (except for 20 hr.). There was no flowering photoperiod. Capsule production and overall plant growth (dry matter) also increased with increasing day length. When tested with nonvarying light and varying temperatures, ranging from 16°/11°C (day/night) up to 28°/22° the number of capsules increased by a factor of 1.3. When tested for productivity in varying moisture regimes, purslane was able to mature capsules in soils of high or low moisture. Zimmerman (1977) reported on the breeding system and seed physiology. Purslane flowers did not open on cloudy days or days below 21°C. When opened, they remained open for 4 hours. The flowers were self-fertile, and under experimentation did not exhibit apomixis. No insects visited the flowers. Mulligan (1972) saw no insect visitors to purslane flowers over a three-year study. These same features of autogamy, no apomixy and lack of insect pollinators were supported by Kim and Carr (1990a). Miyanishi and Cavers (1980) reported evidence of at least 5% outcrossing in purslane and Mulligan (1972) and Zimmerman (1976) proposed that outcrossing is accomplished by wind. Our examination of the flowers showed the pollen to be sticky, not a characteristic of a wind borne process. Kim and Carr (1990b) reported a natural hybrid in which *P. oleracea* was one of the putative parents.

In Zimmerman's study (1977), seed germination remained constant, at over 90%, over a 2.5 yr. period. Vengris et al. (1972) reported the following percentages of germination for seeds: 0.2 year-old, 39%; 1 year-old, 78%; 7 years-old, 59%; 14 years-old, 59%. Muenscher (1955) reported that purslane seeds were viable for at least 40 yr. Zimmerman (1977) found over 60% seed viability after passing them through a house sparrow (*Passer domesticus*). Light was required for germination, but the temperature requirements were variable. Purslane seeds can germinate at 10°C and in a test of overwintering, over 82% of the seed survived a winter in Michigan. Singh (1968) showed that seeds collected in India germinated over a range of 10°–40°C, but did not germinate at 50°C. Vengris et al. (1972) noted that a purslane plant





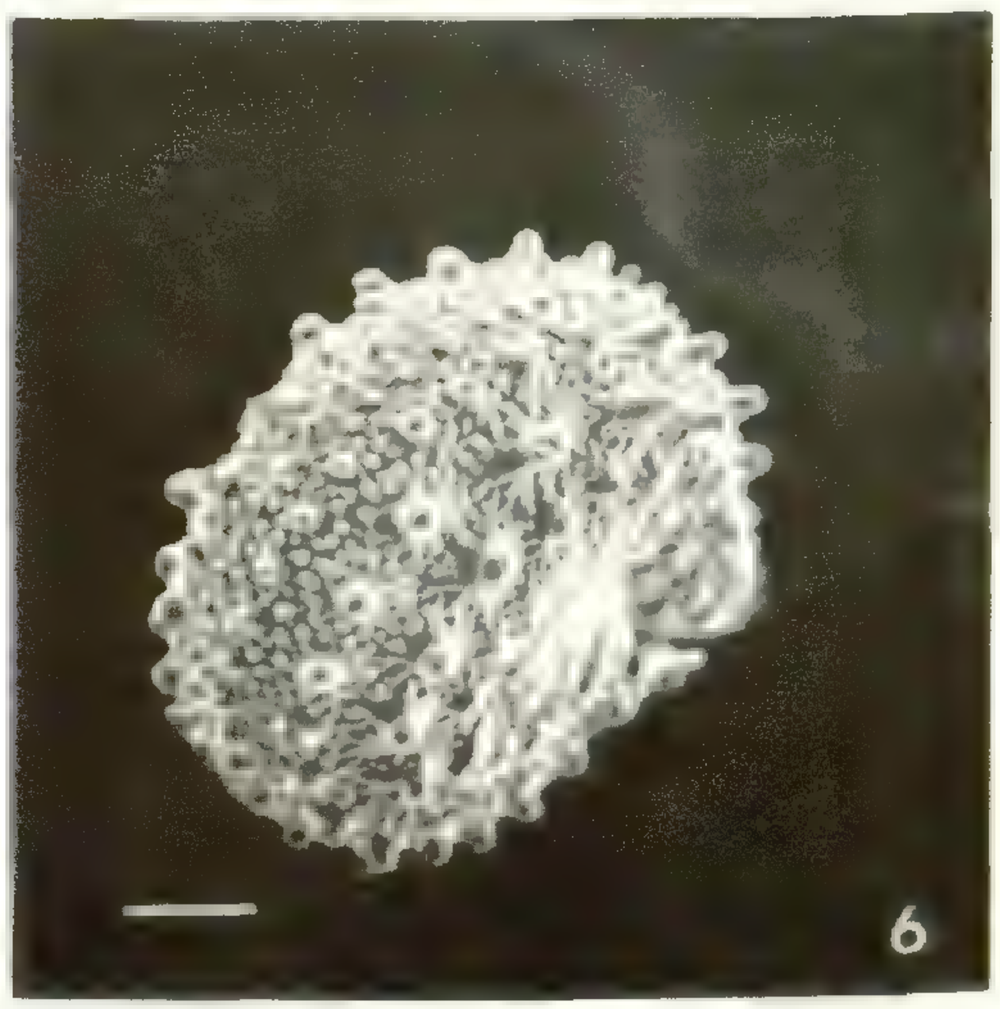




Figure 1. Granulate pattern in *P. oleracea.*

Figure 2. Stellate (S-undulate) pattern in *P. oleracea.*

Figure 3. Stellate (S-undulate) tuberculate pattern of a specimen labelled *P. retusa* that matches Engelmann's lectotype.

of 28 cm produced 6723 seeds after 5–6 weeks of growth (e.g., the first flush of flowers). Zimmerman (1976) estimated that over an entire season a purslane plant can produce 101,625 to 242,540 seeds.

From the above, *Portulaca oleracea* can be characterized as a weed of open, disturbed habitats with nearly a world-wide adaptability and distribution. It grows rapidly, producing flowers, fruits and a large number of seeds within six weeks of germination. It has a wide tolerance of photoperiod, light intensity, temperature, moisture and soil type. Seeds germinate under conditions that enhance the survival of seedlings. The self-compatible breeding system, longevity of seeds, resistance of the seeds to the digestive processes of animals, and the overwintering capacity of the seeds help ensure its survival and distribution. These characteristics have a bearing on the taxonomy of the species as described below.

## TAXONOMY

In an ancient, cosmopolitan species in which autogamy is the rule, local populations possibly reflecting variable morphological and physiological traits can be expected. The fact that the species has not been split into a plethora of microspecies (as defined by Stace, 1989) is surprising. An examination of the two most recent comprehensive monographs, Legrand (1962) and Geesink (1969), show the following: Legrand's treatment of the American species has only three synonyms at the specific level under *P. oleracea.* Geesink's treatment of the Indo-Australian and Pacific species places only two in synonymy. There thus appears to have been a reticence to subdivide *P. oleracea.* Whether this is due to a lack of understanding of the genus or of an appreciation of the variability of this species is unknown. In reality, both reasons probably are contributors. An examination of the works of Legrand and Geesink, cited above, shows several examples of taxonomic/no-

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Figure 4. Raised stellate (S-undulate) pattern without tubercles labelled as *P. retusa.*

Figure 5. Raised stellate (S-undulate) pattern with incipient tubercles, labelled as *P. retusa.*

Figure 6. Granulate pattern with tubercles labelled as *P. retusa.*

menclatural problems in species less widely distributed than *P. oleracea.*

Gorske et al. (1979) provide some insight into the world-wide variability of *P. oleracea* in their numerical taxonomic study. Forty-four ecotypes representing both weedy and cultivated forms from 18 countries were analyzed, using 36 morphological characteristics. The cultivated forms, used for food, were obtained from commercial seed sources in Egypt, France, Norway and the United States. No physiological or cytological characters were included in the study. Three different methods were used in the analysis: the unweighted pair group method of clustering using arithmetic averages, principal component analysis and stepwise multiple discriminant analysis. All three analyses gave similar results and show that the cultivated forms can be separated from the weedy populations. The weedy populations can be divided into three distinct groups: cool temperate, warm temperate to subtropic and humid subtropic to tropic. The Canadian populations fit into the cool temperate. The populations from the upper U.S. fit into the warm temperate to subtropic group while those from the lower U.S. fit into the humid subtropic to tropic group. The effects of selection for cultivation (forming a separate group) are apparent, as well as are the lack of smaller groupings over large geographic areas. That this study over such a large geographic distribution with a large representation of ecotypes showed only three groups that fit a clinal variation from warm humid subtropic to cool temperate, and did not segregate into groups that could be considered as microspecies supports our conclusion that *P. oleracea* is best viewed as a single polymorphic species. As discussed below under the cytology, within the U.S., three cytotypes occur. There is no well-defined cytological correlation with the cool temperate, warm temperate to subtropic and humid subtropic to tropic groups. *Portulaca oleracea* is a weed that exhibits wide geographical, morphological, physiological and cytological plasticity, an obvious reason for its success.

Several names have been proposed as segregates within this complex. One such is *P. neglecta* Mackenzie and Bush, based on a specimen collected by Bush in Courtney, MO in 1900. Type: U.S.A. Missouri, Jackson Co., 24 Aug 1900, *B.F. Bush s.n.* (Holotype: MO!, Isotype: NY!). Courtney no longer exists, having been eliminated by the growth of Kansas City. An examination of the type specimens and seven other specimens identified as *P. neg-*

*lecta* (the only ones received from all loan requests) from MO, KS and MI have vegetative features and seed surfaces typical of *P. oleracea.* The leaves are large, 40 mm by 15 mm; but this is typical for large specimens of *P. oleracea.* In the original description of *P. neglecta,* Mackenzie and Bush (1902) differentiated the new species from *P. oleracea* on the basis of earlier opening flowers; larger size of the plant; larger, broader and thinner leaves and more numerous stamens. He said that *P. neglecta* occurred in MO, KS and AR and is probably what has been called *P. retusa* Engelm. in MN, MO and KS. In correspondence from Aug to Nov 1909, from NY, attached to a herbarium sheet without a plant, N. L. Britton asked Bush for fresh material for study. Bush's reply was that the species grew in rich, sandy bottoms and the floods of the past two years had apparently destroyed the populations. Bush also added that the other form, typical *P. oleracea,* grew in pastures and looked very different. From this exchange, we conclude that the large specimens were either escaped cultivated forms or represented local populations from wet habitats in which the plants grew larger than those in drier pastures. All of the features Mackenzie used to differentiate *P. neglecta* are easily modifiable vegetative features. No specimens have been reported since these initial collections. We conclude that *P. neglecta* Mackenzie and Bush is *P. oleracea* L. and that the former name should be in synonomy under the latter.

In another study of this species, Danin et al. (1978) proposed nine subspecies of *Portulaca oleracea,* based on seed size, seed surface and chromosome number, with the cytotypes having distinct geographic separation. We recognize the need to express infraspecific variation (Matthews et al., 1991, 1992a); and as Stace (1989) concluded, "the provision of a name attracts attention to a taxon." In the genus *Portulaca* each species must be studied to determine which characters are consistent and persistent, a difficult process. Due to the almost cosmopolitan distribution of *P. oleracea* with its adaptability to many habitats, the propensity for self pollination, long term seed viability and the lack of specialized seed dispersal mechanism, this species exists in a myriad of local populations that exhibit morphological and/or physiological variability peculiar to each deme. Since the species is succulent, taxonomic characters have been sought in the more durable structures, such as seed surface. In some species of *Portulaca* these surfaces appear to be consistent and predictable but in the wide-

spread *P. pilosa* the seed surface morphology was neither consistent nor predictable over the geographical range of the species (Matthews and Levins, 1985, 1986; Matthews et al., 1992a, 1992b). Legrand (1962) stated that seed surface characters, particularly in *P. oleracea,* are not dependable because the variation is unpredictable. Each population often presents a different pattern. He concluded that seed surface cannot be used to separate even varieties because infinite transitions are produced between non-tuberculate and tuberculate and between rugose and stellate surface patterns.

We find this same situation in *P. oleracea* where there is a mosaic of seed surface morphotypes. We do not think that these morphotypes should be treated as subspecies. We tend to follow in principle the concept of subspecies as defined by Stuessy (1989) where a subspecies should have several conspicuous morphological differences, should be cohesive geographically and largely allopatric, with multigenic control of the differences. Additionally, there is the possibility of hybridization along contact zones but with markedly reduced fertility of hybrids.

In a subsequent study by Danin and Anderson (1986) on the subspecies of *P. oleracea* in Florida, five subspecies representing three cytotypes were identified and their distributions mapped. Most of these five overlapped both in geographic distribution and in chromosome number. In addition there were several specimens that could not be assigned to any subspecies, implying more variation than had been circumscribed in the nine subspecies already described. These were suggested to be potential hybrids.

This does not mean that seed surface morphology is worthless as a taxonomic character. In some genera it has proven useful in defining subspecies. Walters (1964) in *Flora Europaea* recognized four subspecies of *Montia fontana* (Portulacaceae) based on seed surface morphology and very sharply distinct geographic distributions. Here the morphological character is enhanced by allopatric distributions, a situation not present in the study by Danin and Anderson (1986) of *P. oleracea* in Florida.

We conclude that *P. oleracea* exists as a polymorphic species and is not divisible into subspecies based on seed surface as the primary morphological trait.

Another part of the *P. oleracea* complex is *P. retusa* Engelm., described in 1850 (Gray, 1850) from specimens collected by Lindheimer in the granitic region of the Liano (sic), Llano of western

Table 1. Herbarium sheets of *P. retusa* Engelm. considered as lectotypes.

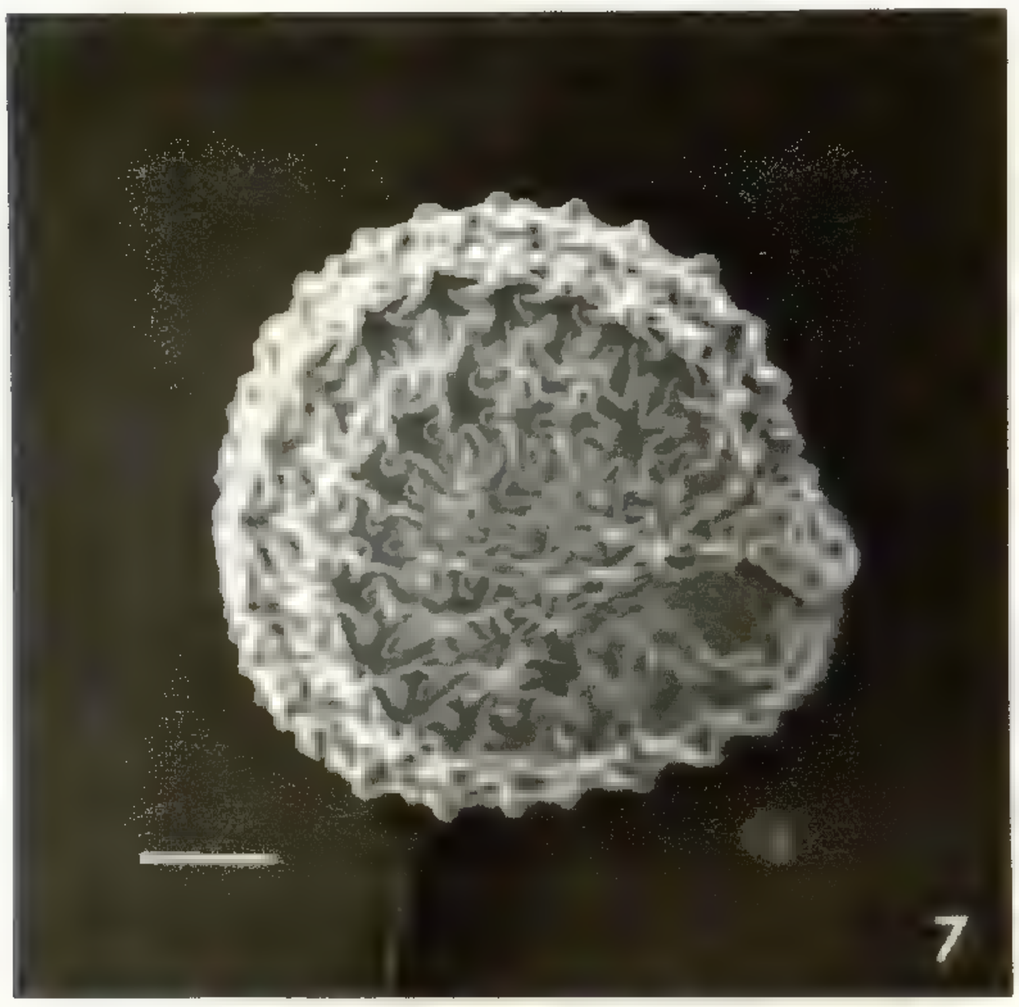
1. *P. retusa* Engelm., Aug 1849. *Engelmann s.n.* (MO, 122802), specimens numbered 8871 and 8872.
2. *P. retusa* Engelm., no date. *Engelmann s.n.* (MO, 122803).
3. *P. retusa* Engelm., no date. *Engelmann s.n.* (MO, 122804).
4. *P. retusa* Engelm., 1849. *Engelmann s.n.* (NY).
5. *P. retusa* Engelm., 1849. *Engelmann s.n.* (NY). Obtained from Princeton in 1945.
6. *P. retusa* Engelm., 1849. *Engelmann s.n.* (NY).
7. *P. retusa* Engelm., Aug 1849. *Englemann s.n.* (GH).

Texas. Engelmann grew plants from seeds sent to St. Louis and distributed specimens to GH and NY. He distinguished *P. retusa* from *P. oleracea* by the former having broader retuse leaves, broader calyx, distinctly tuberculate pale seeds, and larger style with 3–4 short stigmas. He noted that the number of stamens was variable, up to a maximum of 15–17 and that the flowers opened earlier in the day than those of *P. oleracea.*

With the difficulty in assessing herbarium specimens in this genus and with the morphological variability of *P. oleracea* as reported above, the floristic treatments for areas in which both species were reported have relied primarily on the tuberculate seed surface and 3–4 stigmas to distinguish *P. retusa* (Wooton and Standley, 1915; Wilson, 1932; Kearney and Peebles, 1942, 1951; Shreve and Wiggins, 1964; Harrington, 1964; Correll and Johnston, 1970; McDougall, 1973; Martin and Hutchins, 1980; Barkley, 1986; Henrickson, in prep.; Felger, in prep.).

In an earlier study, Matthews and Levins (1986) published an SEM of the seed surface of *P. retusa* showing a tuberculate, S-undulate (raised stellate) pattern as typical for this species. This illustration is reproduced as Figure 3. In the preparation of this treatment for North America, we gathered 121 specimens labelled *P. retusa.* We wanted to compare these to the holotype, but found that Engelmann had failed to designate such and there have been no lectotypes designated. There are seven specimens which qualify for consideration as type material, Table 1.

Sheet one has two plants. One is from the Engelmann collection of Aug 1849 with Engelmann's personal label: "From Texas seeds, cultivated St. Louis." Seeds are present on the specimen, which is noted on the sheet as no. 8871. The other plant on the sheet, with the no. 8872, was collected by Wright in Oct 1849 in western



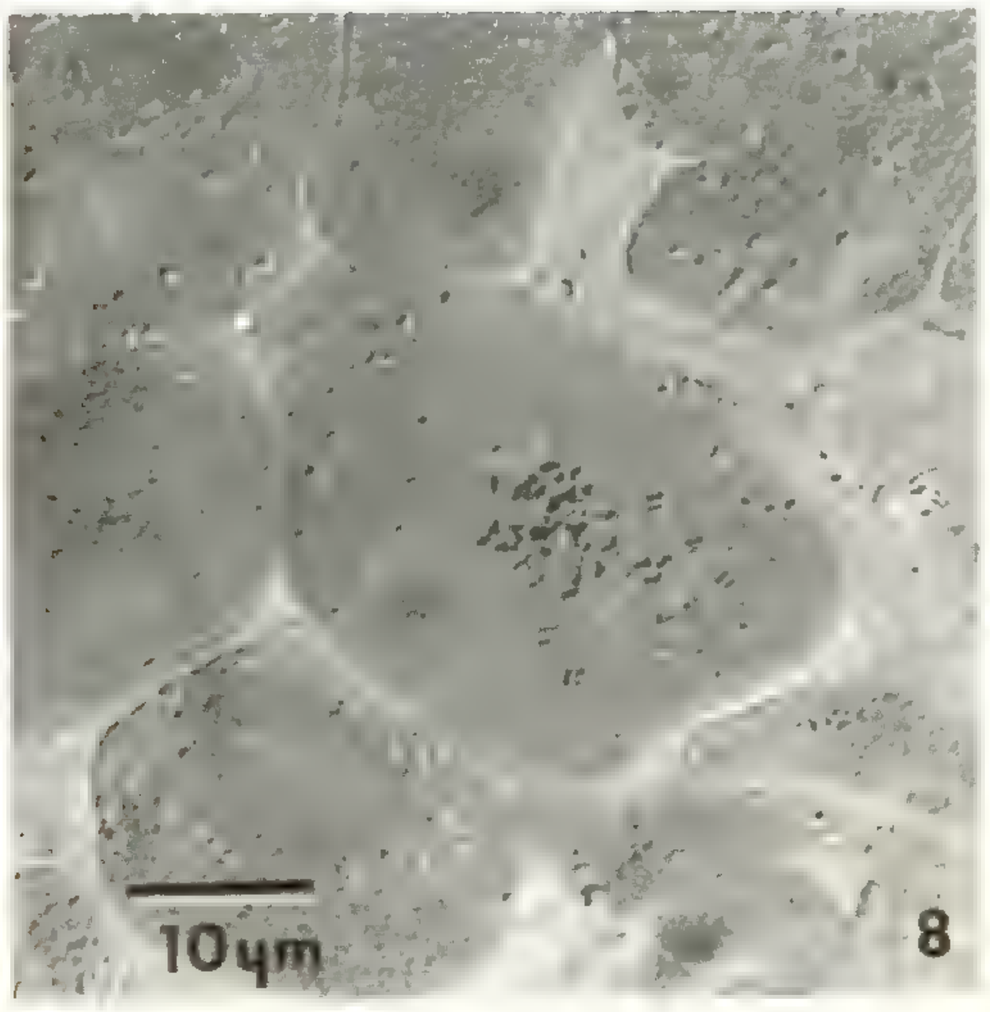




Figure 7. Stellate (S-undulate) pattern with definite tubercles, labelled *P. oleracea.*

Figure 8. Root-tip squash showing $2n = 36$ in *P. oleracea.*

Texas. This plant is also *P. retusa,* but the point at which it was attached to this sheet is uncertain. Sheet 2 has several pieces of plants, including seeds, with Engelmann's handwriting: "From Texas seeds, cultivated St. Louis." Sheet 3 has one large top of a plant, with Engelmann's handwriting: "From Texas seeds, cultivated St. Louis." Seeds are present. Sheet 4 has one large top of a plant, with a label not written by Engelmann: "Texas seeds." Seeds are present. Sheet 5 has one large top of a plant, has an Englemann handwritten label: "From Texas seeds, cultivated." Originally the specimen was at Princeton University but was acquired by NY in 1945. There are no seeds on this specimen, which Legrand annotated as var. *retusa* in 1949. Sheet 6 is a mixed collection. At the top are two small, whole plants annotated by Legrand as *P. lanceolata.* Below are the tops of two plants of *P. retusa,* below which is Engelmann's handwritten label: "From Texas seeds, cultivated." There are two packets of seeds, one at the top and one at the bottom. Sheet 7 has the tops of several plants, has a personal label in Engelmann's handwriting: "From Lindheimer's Texas seeds, cultivated." Seeds are present. Sheets 1 and 7 are the most documentable specimens. Sheets 2 and 3 have no dates, although the date can be implied due to the sequence of numbers. Sheet 4 does not have an Engelmann personal label. Sheet 5 does not have any seeds. Sheet 6 is a mixed collection. Since Engelmann's work was in St. Louis, we designate

Table 2. A comparison of the number of specimens showing the overlap of secondary morphological characteristics used to separate *P. retusa* from *P. oleracea*.

| Specimens Labeled | Seed Size 0.9 mm or More | Seed Size Less Than 0.9 mm | Winged Sepals | Unwinged Sepals |
|---|---|---|---|---|
| *P. retusa* | 83 | 38 | 103 | 18 |
| *P. oleracea* | 58 | 222 | 111 | 169 |

the first specimen, numbered 8871, as the lectotype: UNITED STATES, from Texas seeds, cultivated St. Louis, Aug 1849, *Engelmann s.n.*, MO!, isolectotypes: MO!, GH!, NY!.

Notwithstanding this lack of a holotype, this suite of six specimens (one had no seeds) had the same seed surface characteristics. From our group of 121 specimens labelled *P. retusa,* 59 specimens had the combined raised stellate and tuberculate condition. The others showed various combinations of transitional morphologies, ranging from raised stellate with no tubercles to tuberculate without the stellate pattern. As we examined over 1300 specimens labelled *P. oleracea,* we found 280 specimens with seed surfaces that approached the concept of *P. retusa.* We looked at all specimens with tuberculate or stellate surfaces in an attempt to correlate seed size larger than 0.9 mm, retuse leaf apex, winged (carinate) sepals around the capsule, obtuse vs. acute sepal tips and no. of stigmas/styles, other morphological features that have been used as secondary identifying characteristics in the various treatments cited above. In this broad-leaf group of species, there are many specimens that were well prepared during drying, with packets containing leaves and fruits. We were able to compare the characters enumerated above with the seed surface patterns. The retuse leaf apex is completely unreliable. To illustrate the lack of consistency in the other two characteristics, Table 2 shows the comparison of these features. Many of these 280 specimens were identified originally as either *P. oleracea* or *P. retusa* and later annotated the reverse. We could find no consistency in the shape of the sepal tips nor a definitive number of stigmas/styles. Checking for stigmas/styles in dried portulacas is not very accurate however. Figures 4, 5, 6 and 7 illustrate some of the intermediate patterns of the seed surfaces, which bridge the gaps between Figures 1, 2 and 3 (Table 3). Figures 1 and 2 from the

Table 3. Voucher data for representative specimens of *Portulaca* used for SEM of seed surfaces.

Fig. 1. *P. oleracea* L. Louisiana: Rapides Parish, 19 Jul 1979, *Pias 4345* (NLU).
Fig. 2. *P. oleracea* L. Alabama: Mobile Co., 26 Aug 1965, *Deramus D732* (ALU).
Fig. 3. *P. retusa* Engelm. Texas: Williamson Co., 16 Aug 1961, *Walker 73* (TEX).
Fig. 4. *P. retusa* Engelm. Arizona: Apache Co., 2 Sep 1984, *Mohlenbrock 2434* (ASU).
Fig. 5. *P. retusa* L. Arizona: Navajo Co., 1897, *Zuch s.n.* (US).
Fig. 6. *P. retusa* Engelm. Arizona: Pinal Co., 8 Sep 1929, *Kearney 6002* (ARIZ).
Fig. 7. *P. oleracea* L. Texas: Garza Co., 29 Jul 1967, *Hutchins 1354* (SMU).

southeast show the granulate and obscurely stellate patterns respectively. Figure 3 is the typical "*P. retusa*" type. Figure 4 shows the beginning of the raised stellate pattern, with Figure 5 showing an increase in height. Figure 6 shows a tuberculate pattern emerging from a granulate surface, while Figure 7 shows the beginning of a tuberculate pattern from a completely stellate (no granules), which then merges into Figure 3. Other transitional surfaces can be found, but these serve to show the clinal variation.

Legrand (1962) specifically discussed the concept of *P. retusa.* He dismissed all of the morphological features (seed size, winged sepals and number of stamens) as being influenced by the environment and the season at the time of development. He also noted that there were transitional seed surface patterns between *P. oleracea* and *P. retusa,* saying that he had seen these same forms in plants from the provinces of Salta and Cordoba in Argentina. We observed on specimens he annotated early in his study that he considered *P. retusa* to be a variety of *P. oleracea.* A specimen from NY was annotated in 1949 as var. *retusa,* but by the time he published his monograph in 1962 he had lost confidence in the seed surface characteristic and failed to recognize *P. retusa* as a variety.

Since Engelmann originally cited the granitic region of west Texas as the type locality, we checked the 121 specimens with well defined stellate-tuberculate seed surfaces for habitat and geographic distribution. There were no habitat correlations, the plants being associated with alluvial soil, clay meadows, rocky slopes, granite, rhyolite, limestone, gypsum and dolomite. Geographi-

cally the specimens were distributed from central TX up through the panhandle of TX into OK, southern KS and CO and westward into southern NM and AZ, with transitional forms into the Mojave Desert of CA.

Because of the lack of predictable and persistent morphological features, including seed surface, we conclude that *P. retusa* is a part of the polymorphic *P. oleracea.*

## CYTOLOGY

*Portulaca* is characterized by a sequence of polyploids, particularly in the more geographically widespread species (Matthews et al., 1992a, 1992b). *Portulaca oleracea* shows this sequence also, from a base of X = 9. There are diploid races ($2n = 18$) in Africa (Hagerup, 1932), Central and North America (Danin et al., 1978); tetraploid races ($2n = 36$) in India (Khullar and Dutta, 1973), Central and North America (Danin et al., 1978) and hexaploid races ($2n = 54$) in India (Khullar and Dutta, 1973; Sanjappa, 1978), Africa (Hagerup, 1932; Bouharmont, 1965; Boquar, 1986; Nyananyo and Okoli, 1987), in Europe (Walters, 1964; Bouharmont, 1965) and in North America (Cooper, 1935; Steiner, 1944; Heiser and Whittaker, 1948; Mulligan, 1961; Danin et al., 1978) and Hawaii (Kim and Carr, 1990). In addition, Sharma and Bhattacharyya (1956) reported $2n = 45$ from India and Sugiura (1936) reported $2n = 52$ from Japan. The North American counts of $2n = 54$ have been scattered geographically from Wisconsin (Cooper, 1935), Virginia (Steiner, 1944), California (Heiser and Whittaker, 1948; Danin et al., 1978), Ontario (Mulligan, 1961). In addition, Danin et al. (1978) reported $2n = 36$ from California. Danin and Anderson (1986) reported in their study of the subspecies of *P. oleracea* in Florida the occurrence of $2n = 18$, 36 and 54. No counts were made for this study but numbers were projected based on the previous report by Danin et al. (1978) correlated with the identification of the subspecies.

We wanted to determine the chromosome number from a variety of geographic areas to determine if a correlation existed between geography and cytology, when compared to the above data. We also wanted to publish a photograph of the chromosomes for a North American collection. Photographs of the chromosomes of *P. oleracea* are scarce in the literature. Some early reports were accompanied by camera lucida drawings (Cooper, 1935;

Steiner, 1944). There is a photograph of a meiotic figure by Kim and Carr (1990) from Hawaii. Danin et al. (1978) provided the most comprehensive study of the North American distribution, but published no photographs to document the counts. We can understand the reason for this. After a survey of 20 plants from CA, NM, IL, NC and SC involving over 250 root tip preparations we have been unable to achieve a high quality figure for photography. Baquar (1986) stated, "The chromosomes in general are tiny, threadlike, forming clusters and are difficult to spread for karyological studies." Our results are not different from these other investigators. Only two other papers have photographs of the chromosomes of *P. oleracea*; Khullar and Dutta (1973) from India and Nyananyo and Okoli (1987) from Africa. We were able to obtain 10 counts of $2n = 54$ from IL. Ninety-one counts from CA, NM, NC and SC were $2n = 36$. There appears to be a tendency for the hexaploid ($2n = 54$) to occur in the northern part of North America. However before any conclusions can be drawn, further counts from the United States and Canada would have to be made, and these should be compared to the counts from upper latitudes in Europe. Counts of $2n = 54$ have been reported from Africa and India. The best figure we produced is shown in Figure 8, a $2n = 36$ from SC. Voucher specimens are on file at UNCC.

## ACKNOWLEDGMENTS

We wish to thank the McMillan Greenhouse and Conservatory at UNC Charlotte for the maintenance of live plants and S. Boyd (RSA) and M. Basinger (SIU) for collection of live material. Frank Machado, J. Arvey, S. Chapat and Dr. G. Windholz assisted in translation.

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RHODORA, Vol. 95, No. 882, pp. 184–187, 1993

# *PORPHYRA AMPLISSIMA* (KJELLMAN) SETCHELL *ET* HUS: NEW RECORDS OF AN "ARCTIC" SEAWEED IN SOUTHERN MAINE, NEW HAMPSHIRE AND NORTHERN MASSACHUSETTS[1]

EDWARD J. HEHRE[2] AND ARTHUR C. MATHIESON

The occurrence of *Porphyra amplissima* (Kjellman) Setchell *et* Hus in the southern portion of the Gulf of Maine represents a significant extension of its previously known range. Recent accounts limit this species to Norway and Spitzbergen in the Eastern Atlantic (South and Tittley, 1986) and to the Arctic, Maritime Provinces of Canada, and coastal Maine (Bird and McLachlan, 1992). Taylor (1957) included this species as *Porphyra miniata* (C. Agardh) C. Agardh var. *amplissima* (Kjellman) Rosenvinge, citing the arctic and Maine coasts as its range in North America. However, Taylor's vague description of var. *amplissima* as a distinct entity and the lack of any published references pertaining to the Maine records of this taxon have previously cast doubt as to its occurrence in this region. The recent account (Bird and McLachlan, 1992) of this species from the Atlantic Coast of Nova Scotia and lower Bay of Fundy has provided the impetus to search for its presence in the Gulf of Maine. The distribution of *Porphyra amplissima* in New England and the southern part of the Bay of Fundy is substantiated by an examination of *P. miniata* specimens deposited in the Farlow Herbarium, Harvard University (FH) and the Hodgdon Herbarium, University of New Hampshire (NHA).

The majority of our collections of *Porphyra miniata* from Campobello (Stone et al., 1970) and the Wolf Islands (Hehre et al., 1970), both of which are in the southern Bay of Fundy, are without a doubt *P. amplissima*. In addition, we have records of *P. amplissima* from the nearshore open coast of Maine (from Cutler to York), New Hampshire, and as far south as Cape Ann, Massachusetts. We have also recorded *P. amplissima* from several off-

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[1] Scientific Contribution Number 1815 from the New Hampshire Agricultural Experiment Station; also issued as Contribution Number 277 from the Jackson Estuarine Laboratory/Center of Marine Biology.

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shore islands in Maine (e.g., Boon, Hurricane, Smuttynose, and Two Bush) and within estuarine sites near North Lubec, Maine and Dover-Portsmouth, New Hampshire. The New Hampshire sites are within the outer reaches of the Great Bay Estuary System where strong tidal currents occur, simulating open coastal environments (cf. Mathieson et al., 1977, 1983; Reynolds and Mathieson, 1975). The estuarine tidal rapid at Dover Point (approximately 8.5 miles inland) represents the innermost estuarine collection. The presence of *P. amplissima* from Pigeon Cove on Cape Ann (Massachusetts) is of interest for two reasons: this is the apparent southern limit of the taxon in the Western Atlantic; our collections include beautiful specimens collected by Mary Hitchcock, ca. 1900.

Both *Porphyra amplissima* and *P. miniata* are primarily "arctic" species whose southern distributional limits reach northern Massachusetts. They are both annuals (April–November), with identical reproductive phenologies (May–November). The plicate nature of the thallus and the intermixed mosaic of carposporangial and spermatangial tissue on the margins of the blade serve to distinguish *P. amplissima* from *P. miniata* (cf. Bird and McLachlan, 1992). The latter criterion had been used previously to describe *P. miniata* (Taylor, 1957). Our sublittoral data for *P. amplissima* (i.e., 0–30 feet) agree with those of Bird and McLachlan (1992).

The marine algal flora of New Hampshire has been studied in detail during the past 25 years (see Mathieson and Hehre, 1986). Based upon these studies we believe that *Porphyra amplissima* is an uncommon species that occurs sporadically in this part of its range. *Porphyra miniata* is definitely the more common of the two species in the southern Gulf of Maine, but *P. amplissima* becomes increasingly more prevalent as one goes east along the Maine coast towards the Bay of Fundy. Further studies are needed before we can ascertain the importance of *P. amplissima* to the marine algal flora of Maine.

ACKNOWLEDGMENTS

We would like to express our sincere appreciation to the personnel of the Farlow Herbarium of Harvard University for their assistance and loan of herbarium specimens.

REPRESENTATIVE SPECIMENS: CANADA: **New Brunswick, South Wolf Island**—*R. A. Stone & E. J. Hehre,* 4 June, 1968 (NHA *13,500*); *E. J. Hehre & J. R. Conway,* 13 August, 1968 (NHA *14,051 & 14,052*). **Campobello Island**—East Head Harbor, *E. Hehre,* 21 May, 1966 (NHA *1,258*); Harbour de Loutre, *R. A. Stone & E. J. Hehre,* 14 June, 1967 (NHA *9,141*); *J. R. Conway, E. J. Hehre, R. A. Stone & R. A. Fralick,* 18 May, 1968 (NHA *13,349*); Herring Cove, *E. J. Hehre,* 20 May 1966 (NHA *4,626*); *J. R. Conway & E. J. Hehre,* 11 August, 1968 (NHA *14,099*); Little Duck Pond, *R. A. Stone, E. J. Hehre* and *R. B. Pike,* 5 June, 1968 (NHA *13,350*); *E. J. Hehre & J. R. Conway,* 12 August, 1968 (NHA *14,149 & 14,150*); Mulholland's Bend, *R. A. Stone & E. J. Hehre,* 15 June, 1967 (NHA *9,261 & 9,270*); *E. J. Hehre & J. R. Conway,* 9 August 1968 (NHA *14,125*); Raccoon Point, *E. J. Hehre & R. A. Stone,* 16 June, 1967 (NHA *9,175*); *E. J. Hehre & J. R. Conway,* 10 August, 1968 (NHA, *14,177*); Whiterock Cliffs, *R. A. Stone & E. J. Hehre,* 17 June, 1967 (NHA *9,313*). UNITED STATES. **Maine** (nearshore)—Pirates Creek, North Lubec, *D. Lavoie,* 21 May, 1966 (NHA *1243*); Cutler, *F. S. Collins,* 6 July, 1902 (FH); East Machias, *G. Vagenas,* 21 May, 1966 (NHA *1,245*); Long Sands, York, *J. Kotheimer,* 6 June, 1966 (NHA *1,255 & 1,256*); (offshore islands)—Hurricane Island, Penobscot Bay, *J. Hambrook,* 29 May, 1986 (NHA *49,943*); *J. Hambrook* (−10 to −20 feet), 1 June, 1986 (NHA *49,935*); Two Bush Island, near Hurricane Island, Penobscot Bay, *J. Hambrook,* 12 June, 1985 (NHA *49,164*); Boon Island, York (−20 to −30 feet), *A. C. Mathieson,* 30 June, 1976 (NHA *27,897 & 27,932*); Smuttynose Island, Kittery, *A. C. Mathieson,* 19 November, 1976 (NHA *39,505*). **New Hampshire** (nearshore)—Jaffrey Point (Fort Stark), New Castle, *E. J. Hehre & A. C. Mathieson,* 9 August, 1967 (NHA *10,321*); Rye Ledge, Rye, *J. Shipman & J. Conway,* 21 June, 1966 (NHA *1,275*); (estuarine)—Fort Constitution (Fort Point), New Castle (0.8 miles inland), *J. R. Conway & J. Shipman,* 22 June, 1966 (NHA *1,277*); *E. J. Hehre,* 29 May, 1967 (NHA *9,035*); *E. J. Hehre,* 23 June, 1967 (NHA *8,957*); Bridge at Rte. 1 Bypass, Portsmouth, west bank (4.0 miles inland), *E. J. Hehre,* 29 May, 1967 (NHA *9,036*); Dover Point (Hilton Park), Dover, junction of Little Bay and Piscataqua River (8.6 miles inland), *E. J. Hehre,* 23 June, 1967 (NHA *9,392*); *N. B. Reynolds,* 15 May, 1969 (NHA *15,491*); *N. B. Reynolds,* 17 June, 1969 (NHA *15,492*). **Massachusetts** (nearshore)—Pigeon Cove, Cape Ann, *E. J. Hehre,* 23 June, 1966 (NHA *1,269*); *M. Hitchcock,*

ca. 1900 (NHA *1,244, 1,246, 1,247*); Halibut Point, Cape Ann, *I. M. Lamb* and *M. Zimmermann,* 17 June, 1962 (FH, A-*455*); Nahant, *F. S. Collins,* 24 June, 1882 (FH).

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RHODORA, Vol. 95, No. 882, p. 188, 1993

# NEW ENGLAND NOTE

## SOME NEW RECORDS FOR NEW ENGLAND STATES. III.

RAY ANGELO

These previously unreported records for New England states have come to the attention of the Club's Curator of Vascular Plants in the course of executing his curatorial duties. The first and second such reports appeared in Rhodora 91: 342–344 (1989) and 92: 294–296 (1990).

These records are intended to represent the first published evidence of these species in the state, not necessarily the first collection. The records cited here are for specimens that have been accessioned by the Club herbarium (NEBC). Their newness has been determined by making use of the most current floras, checklists and other readily available published sources which are based upon public herbarium records.

### NEW RECORD FOR MAINE

**Glyceria acutiflora** Torr. [Poaceae]

Limington, ME (York Co.); *Samuel N.F. Sanford*; August 6, 1925; "Peqaket Lake. *In* shallow water."

### NEW RECORD FOR RHODE ISLAND

**Celastrus orbiculatus** Thunb. [Celastraceae]

Block Island, RI (Washington Co.); *Robert Marks*; August 31, 1974. [This specimen, originally identified as Celastrus scandens L., has been reidentified by R. Angelo. This species also collected from Warwick, RI (Kent Co.), *David E. Boufford* (#*25287*) & *Ray Angelo* (1990).]

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RHODORA, Vol. 95, No. 882, pp. 189–190, 1993

# A TAXONOMIC STUDY OF *ARISTIDA STRICTA* AND *ARISTIDA BEYRICHIANA*; ADDENDUM[1]

ROBERT K. PEET

I have discovered an additional isotype of *Aristida beyrichiana* Trinius & Ruprecht held at MO (2874410). The label includes the specific date and location of the collection, information lacking on the labels of the other known type material. The specimen comes from the Bernhardi Herbarium (see D'Arcy, 1971) and is mounted together with a collection of *Aristida stricta* Michaux, apparently collected by Nuttall. The label includes the initials CB, and J. M. Greenman annotated the collection as that of Charles Beyrich. This Beyrich collection has the same degree of spikelet immaturity as the isotypes in L and US. The label reads "6/1 33," which is consistent with the fact that Beyrich collected in the southeastern states only in 1833 (Sayre, 1975), and the June 1 date is consistent with the immaturity of the spikelets. The label indicates that the collection is from the area near Ebenezer. Presumably this is the Ebenezer located in Effingham County, Georgia, approximately 25 miles north of Savannah. The isotype in L indicates the type collection is from Georgia. Ebenezer, while already a declining town in 1854 (Baldwin and Thomas), is one of the oldest villages in Georgia and, being on the main route of travel up the Savannah River, was visited by traveling botanists such as William Bartram (Harper, 1958). *Aristida beyrichiana* is known for Effingham County, Georgia (EHCV 571). There was in the early 1800's another village of Ebenezer, Georgia in Morgan County (Baldwin and Thomas), but this location is out of the range of *A. beyrichiana* and is much less likely to have been visited by Beyrich.

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[1] Peet, R. K. 1993. A taxonomic study of *Aristida stricta* and *A. beyriciana*. Rhodora 95: 25–37.

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RHODORA, Vol. 95, No. 882, p. 191, 1993

# THIRD ANNUAL RICHARD AND MINNIE WINDLER AWARD WINNER ANNOUNCED

On April 16th, at the annual meeting of the Association of Southeastern Biologists (ASB), the third annual Richard and Minnie Windler Award was presented to Warren Frank Lamboy. Dr. Lamboy is a Research Associate in the germ plasm lab of the Plant Genetic Resources Unit of the New York State Agricultural Experiment Station, Cornell University in Geneva, NY. His paper, "*The Taxonomic Status and Probable Origin of* ASTER CHLOROLEPIS, *a Southern Appalachian Endemic,*" was published in the March 1992 issue of CASTANEA, the quarterly publication of the Southern Appalachian Botanical Society (SABS).

In the research described in this paper, the author uses traditional, phytogeographical, cytological and numerical techniques to clarify the taxonomic status and explore the relationship between two species of the genus *Aster,* the endemic *Aster chlorolepis* and its close relative, *Aster divaricatus* L., a species ranging from Northern Alabama and Georgia to Southern Canada. Dr. Lamboy's data lead him to the conclusion that *A. chlorolepis* is an autotetraploid derivative of *A. divaricatus.* The publication represents a portion of a Ph.D. dissertation submitted to the University of Illinois, Urbana.

The Richard and Minnie Windler Award was established in April of 1990 at the annual meeting of the Southern Appalachian Botanical Society in Towson, Maryland, by Dr. Donald R. Windler as a memorial to his parents. The award is presented annually to the author(s) of the best paper in systematic botany published in the previous year's volume of CASTANEA. The eligible papers fall into the broad area of plant systematics, including floristic, experimental, revisionary, and nomenclatural studies. This year's awardee received a framed certificate and a monetary award of $200, funded by an endowment administered by the Society.

The winner is selected by a committee comprised of the three most recent systematics editors of the journal, after their terms as editor have expired. The present committee is chaired by Dr. David Whetstone of the University of Jacksonville. The other committee members are Dr. James Matthews of the University of North Carolina at Charlotte and Dr. Robert Haynes of the University of Alabama at Tuscaloosa.

## 1994 NEBC AWARD FOR THE SUPPORT OF BOTANICAL RESEARCH

The New England Botanical Club will offer an award of $1,000 in support of botanical research to be conducted in relation to the New England Flora during 1993. This award is made to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany, biosystematics, plant ecology, or plant conservation biology, although proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to Rhodora for possible publication subject to standard review processes.

The 1993 Award recipient was Ms. R. Deborah Overath of the University of Georgia, in support of her work on the effects of apomixis on genetic variation in *Amelanchier laevis.*

Applicants must submit a proposal of no more than three double-spaced pages, a budget (the budget will not affect the amount of the award), a curriculum vitae, three copies of the application, and two letters in support of the proposed research, one from the student's thesis advisor. Proposals and supporting letters must be received no later than March 1, 1994. The recipient of the award will be notified by April 30, 1994. Proposals should be sent to: Awards Committee, The New England Botanical Club, 22 Divinity Ave., Cambridge, MA 02138.

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# Rhodora

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# RHODORA



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**Cover Illustration**

*Amelanchier nantucketensis* Bickn., the Nantucket Shadbush, is found only on dry moors, pine-barrens and pond margins on Nantucket and Martha's Vineyard Islands. A surculose, loosely colonial shrub to 2 m, this member of the Rosaceae is currently a candidate plant for federal listing. Original artwork by Alison Dibble.


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# TAXONOMIC REVISION OF *ARCTOMECON* TORR. & FREM.

DEANNA R. NELSON AND STANLEY L. WELSH

## ABSTRACT

The genus *Arctomecon* Torr. & Frem. is reviewed, its three species, *A. humilis* Coville, *A. californica* Torr. & Frem., and *A. merriamii* Coville, are provided with a diagnostic key, described, and discussions of their peculiar habitat requirements and other pertinent information are included.

Key Words: *Arctomecon, A. humilis, A. californica, A. merriamii,* habitats, geography, Mohave Desert

## INTRODUCTION

The genus *Arctomecon* Torr. & Frem. (Papaveraceae) is composed of three distinctive species: *Arctomecon californica* Torr. & Frem., *A. humilis* Coville, and *A. merriamii* Coville. All are gypsophilous species endemic to northern portions of the Mojave Desert regions of the southwestern United States, where their distributions are restricted to peculiar edaphic situations. Plants of all of the species are perennial herbs with long taproots, woody caudices, and tufts of basal leaves. Flowers are large and showy with petals white or yellow. All three species are considered to be rare, but only *A. humilis* is presently listed under stipulations of the Endangered Species Act of 1973 as amended (USFWS, 1979). Recent inventories of populations of *A. californica* and *A. merriamii* revealed losses in habitat, due primarily to development and urban expansion in the Las Vegas area, which has resulted in elimination of entire subpopulations. Need for pro-

tection of all species in the genus under the Endangered Species Act is indicated.

The generic name *Arctomecon* was regarded as neuter by Torrey, hence the name *californicum*. It is regarded here as feminine, following the example for Greek nouns with the "-on" termination cited in Stern's Botanical Latin (1983, p. 84), and the termination of the specific epithets agree with that gender. When included in quotes the original form, as treated by Torrey and others, is followed.

## HISTORY

The type of the genus *Arctomecon* (Greek arktos, of bear; and mekon, a poppy, from the fancied resemblance of the hairy leaves with the lobes armed with a long trichome to a bear's foot), and its initial species *californica* (of Alta California, then a portion of Mexico), was collected by John Charles Fremont on his second expedition of exploration of the American West. On 3 May 1844 they reached the springs at "*las Vegas* [The Meadows]—a term which the Spaniards use to signify fertile or marshy plains, in contradistinction to *llanos,* which they apply to dry and sterile plains. Two narrow streams of clear water, four or five feet deep gush suddenly, with a quick current, from two singularly large springs; these and other waters of the basin, pass out in a gap to the eastward. The taste of the water is good, but rather too warm to be agreeable; the temperature being 71° in the one, and 73° in the other. They, however, afforded a delightful bathing place" (Fremont, 1845, p. 266). There he collected the plant that became the type specimen "on the banks of a creek." The water from the two springs coalesced into a stream—the only one in the vicinity (Welsh, 1993).

In 1874, Charles Christopher Parry collected, near St. George, Utah, a "showy Papaveraceous plant with nodding white flowers" (Parry, 1875). Parry identified this plant as *A. californica,* but recognized that it differed from Fremont's earlier, solitary collection, in its "less hairy leaves, four (not six) valved capsule and more caespitose habit." Parry forwarded a portion of his collection (he took plants in sets for later distribution through exchange or sale) to Dr. Asa Gray at Harvard University. Dr. Gray also identified the Parry materials as *A. californica* (Gray, 1877). Neither Parry nor Gray had noted that the Fremont materials were

described as having yellow petals. Parry's materials were noted as distinctive by Coville (1892) who published them as belonging to a newly erected species, *A. humilis* Coville, but not until two years following the death of Parry (Welsh, 1988). In that same publication (Coville, 1892) a second species with white flowers, *A. merriamii* Coville, was proposed for the genus. It was based on specimens taken by Vernon Bailey west of Vegas Ranch in Lincoln County, Nevada in 1891 (Mozingo and Williams, 1980). Thus, the genus, as it is currently recognized, was fully constituted by 1892.

## TAXONOMIC AFFILIATIONS

*Arctomecon* differs from other papaveraceous genera present in the Mojave Desert (*Argemone, Platystemon*) in general habit and gross morphologic features. Its species are the only members of the poppy family, in North America at least, recognized as gypsum restricted. The three species share ample characters to readily demonstrate their affinity, while the differences between the species are substantial enough to provide clear taxonomic units. All three species can be readily recognized by their foliage; the dense rosette of relatively long, broad, green leaves appears very "extravagant" in comparison to that of most plants of the warm desert regions. Affinities of the genus to others of the American southwest have not been resolved.

The species differ morphologically from each other on the basis of arrangement of flowers in the inflorescence, flower color, status of the petals following anthesis, number of locules per ovary, outline of apical margins of the leaf, amount and kind of foliar vestiture, and the overall stature of the plant. Distinct morphological differences, when taken with the geographic isolation of the species from each other, suggest that the separation of the taxa was not a recent event.

Raynie et al. (1990) report alkaloid content of the three *Arctomecon* species. Total number of alkaloids was greatest for *A. humilis,* with 14 unique alkaloids. Eight were detected in the tissues of *A. californica* and five in *A. merriamii.* Three alkaloids were found to be common to all species of the genus. Allocryptopine and protopine were major alkaloids in all species, while 12-methoxyallocryptopine (a new protopine-type alkaloid isolated during the study and presently known only from *Arctomecon*)

was found in lesser quantities. It is uncertain what clues alkaloid composition can provide to understanding the evolutionary relationships between this genus and other Papaveraceae, and between the species in the genus. The larger numer of alkaloids in *A. humilis* may suggest that the species is ancestral to the others (Raynie et al., 1990). To date, the chemical and morphological criteria have not provided evidence of a close relationship of this genus to others in the family.

## DISTRIBUTION

All species of *Arctomecon* are endemic to the northern margin of the Mojave Desert regions of the southwestern United States (Figure 1). The range of *A. humilis* is the most restricted of the three. It is presently known to be limited to an archipelago of less than a dozen sites, all within a few miles of St. George, Utah. Plants are strictly limited to gypsic outcrops of the Moenkopi Formation, primarily to the Shnabkaib Member, but occasionally extending downward to the Middle Red Member and upward to the Upper Red Member. The low, rolling terrain formed by these gypsum outcrops makes these areas popular for off-road vehicle use. All accessible sites are heavily impacted by off-road vehicular traffic which rapidly destroys cryptogamic soil crusts and compacts the substrate. It is noted that Kearney and Peebles (1960) cite *A. humilis* from northern Arizona, and an equivocal specimen cited from there is present at BRY, but probably it came from Utah. Recent investigations, including those by the authors, have not located this species in Arizona, although it has been found within one km of the Utah-Arizona boundary.

The ranges of *A. californica* and *A. merriamii* appear to overlap in the Las Vegas area, but the species do not occur together, probably due to differences in habitat requirements. In the Las Vegas area *A. californica* occurs on Quaternary Alluvium, often on ancient gypsic playa remnants. To the east, near Lake Mead, it is on other alluvium, but also on the Moenkopi Formation, and, in adjacent Arizona, it evidently occurs on gypsic limestones. In comparison, *A. merriamii* seems to prefer the gypsic limestones and gravels, and mainly occurs in numerous, small, disjunct subpopulations. Many habitats that appear to be habitable by the species of this genus do not support any of the plants. The reasons for the paucity of the plants are unknown. Several known sites

Figure 1. Habit sketch of *Arctomecon humilis* Coville.

of former habitation of both *A. californica* and *A. humilis* have been obliterated by construction, with pavement and structures now occupying the sites. It is believed that some other populations may have recently disappeared, especially in the Las Vegas area. The California bearclaw poppy occurred as recently as the mid

1980's in a vacant lot in a subdivision along Craig Road in Las Vegas, growing on an evidently saline playa remnant.

The range of *Arctomecon merriamii* extends from Death Valley on the west to the Spring Mountains of Nevada on the east. The species has been reported from approximately 20 sites within Death Valley National Monument, and from three or four mountain ranges in Nevada and near Ash Meadows, Nevada. One population is known from within the Las Vegas, Nevada, city limits. This population has been closely monitored by the authors and presently includes 15 individuals. The site is heavily impacted by construction on adjacent lots and its future is in doubt.

## ECOLOGY

All three species of *Arctomecon* have been observed on heavily gypsic substrates. Since all records of occurrence of *A. humilis* and *A. californica* have been from such substrates, it seems reasonable to assume that this affinity to gypsum is obligate for these species. The situation with *A. merriamii* is not so clear. It is known from both definitely gypsic sites and from limestones where the presence of gypsum has not been demonstrated. Thus, it might be considered a facultative gypsophile.

Gypsum content of soils at four sites occupied by *A. humilis* was determined to be from 27 to 51 percent by weight (Nelson, 1989) and at five *A. californica* sites ranged from 36 to 69 percent (Meyer, 1987). Gypsum content of soils at four sites occupied by *A. merriamii* was determined to be from 2 to 8 percent by weight. The soils on sites occupied by *A. humilis* and *A. californica* tend to have very low bulk densities due to the presence of sponge gypsum and often have a heavy cover of cryptogams (Meyer, 1987; Nelson, 1989). It has been suggested that the unique chemistry of gypsic sites, especially the high sulfur content, is a primary factor responsible for the evolution of gypsophile endemics (Parsons, 1976). Meyer (1986) found gypsophiles to occur only where gypsum content was sufficiently great to effect physical properties of soil, while much smaller amounts of gypsum would still create high sulfate levels.

Because of their apparent obligate affiliation with gypsic soils, both *A. californica* and *A. humilis* are not found growing in close association with the creosote bush-dominated desert shrub com-

munity typical of the Mojave Desert (Meyer, 1987; Nelson, 1989). They are, instead, found with a complement of other gypsum-tolerant species, including shadscale [*Atriplex confertifolia* (Torr. & Frem.) Wats.], burrobush (*Hymenoclea salsola* T. & G.), indigo bush [*Psorothamnus fremontii* (Torr.) Barneby], ephedra (*Ephedra torreyana* Wats.), and Anderson wolfberry (*Lycium andersonii* Gray). Plant species associated with *A. merriamii* are much more diverse. It has not only the widest geographic range, and the broadest tolerance with regard to substrate, but it also has the broadest elevational tolerance (610 to 1710 m). The elevational range of *A. humilis* is 750 to 1070 m, and that of *A. californica* is between 550 and 950 m. A solitary record of *A. californica* is known from Utah, from the Moenkopi Formation, on the Coalpits Wash road, where it might have been recently introduced.

All of the species flower in April and May, with *A. humilis* reaching the peak of flowering in early May, somewhat later than for the other species. Pollinating agents observed at flowers of low bearclaw poppy include both honey bees (*Apis mellifera*) and native ground nesting bees. Experimental hand pollinations have shown that this species relies almost exclusively on outcrossing with neighboring plants (Nelson, 1989). Information on pollination ecology of the other species is lacking.

Large plants of *Arctomecon humilis* may produce as many as 400 flowers, of which 70–75 percent are expected to mature fruit. Capsules generally produce at least 23 fully developed seeds. Petals of this species are persistent, surrounding the developing capsule as they dry. The mature capsule abscisses from the pedicel several millimeters below the mature ovary and the fruit enfolded by marcescent petals falls free. Some seeds, those falling from capsules still attached to the plant, are deposited among the leaves of the rosette and elsewhere near the plant base. Other seeds are scattered for some distance from the plant when the fruit abscisses and is tumbled across the land surface, propelled by the wind against its petal "wings."

Studies of populations of *A. californica* (Meyer, 1987) and *A. humilis* (Nelson, 1989) demonstrate drastic year-to-year fluctuations in population density. Data suggest that, for both species, such volatile cycles are primarily the result of a relatively short lifespan (individuals surviving the first year may be expected to live an average of four to five years) coupled with irregular occurrence of germination events. Meyer (1987) found that years

with sufficient winter rainfall to assure significant establishment of *A. californica* seedlings may occur as much as nine years apart. During a four year study of populations of *A. humilis* only a single germination event was observed (Nelson, 1989). Both species appear to rely on high reproductive output and the maintenance of a large reservoir of long-lived seed in the soil in order to persist. Separation of organic material from soil collected near *A. humilis* plants, using a flotation technique, revealed a large quantity of seed "entrapped" within cryptogamic soil crusts. This suggests the importance of protecting these soil surfaces in order to maintain soil seedbanks critical to the survival of populations. Dynamics of population densities in *A. merriamii* have not been documented.

## TAXONOMY

**Arctomecon** Torr. & Frem. in Frem. Rep. Expl. Exped. Oreg. & N. Calif. 312. 1845.

TYPE SPECIES: *Arctomecon californica* Torr. & Frem. *in* Frem.

Perennial herbs from a subligneous caudex and long taproot, subacaulescent, caulescent, or subscapose; leaves mostly in a basal rosette, some typically cauline, usually cuneate, long-hirsute, mostly toothed apically and the teeth spinulose-tipped; flowers large and showy, solitary, or borne in leafy-bracteate cymes, nodding in bud, becoming erect at anthesis; sepals 2 or 3, caducous; petals 4 or 6, white or yellow; anthers basifixed, oblong, opening longitudinally; pistil 1, the carpels 4 or 5 (6), the styles obsolete or united and less than 1.5 mm long, the stigmas connate, with 4–6 lobes; ovary unilocular; capsules acrocidal along 4–6 sutures; seeds strophiolate.

1. Flowers yellow, (5) 6–20, in a paniculiform cyme; plants subacaulescent, of Clark County, Nevada, and Mohave County, Arizona (apparently introduced in Washington County, Utah) ..... *A. californica*
1. Flowers white, solitary or 2–5 (7); plants variously distributed ..... 2
    2. Petals 4; plants scapose; flowers 2–5 in a paniculiform cyme; plants of Washington County, Utah ..... *A. humilis*
    2. Petals 6; plants subacaulescent; flowers 1 or 2 (3–7) in a greatly shortened cyme, the elongated pedicels scapose;

plants of Death Valley, California, and Nye, Clark, and Lincoln counties, Nevada ..... *A. merriamii*

**Arctomecon humilis** Coville Proc. Biol. Soc. Wash. 7: 67. 1892. (Figure 1)

Low or dwarf bearclaw poppy.

Type locality: "In 1874 Dr. C. C. Parry collected in the vicinity of St. George, Utah, an *Arctomecon,* which Dr. Gray referred to *A. californicum.* The material now at hand shows that it is distinct both from the original plant of Fremont and from the species just described [i.e., *A. merriamii*]. It differs from the former in its smaller size throughout, less hairy leaves, fewer flower parts, white petals, dilated filaments, and the presence of a style; from *A. merriamii* in its smaller size and more scanty hairs, more than 1-flowered peduncles, fewer flower parts, persistent petals, and obovate, several times shorter than the capsule" (Coville, 1892).

Type: "Flora of Southern Utah, &c. Arctomecon humile, Coville, non Arctomecon Californicum Torr. & Fremont, *C. C. Parry 6,* 1874" (HOLOTYPE GH; ISOTYPE NY!; frag. US!).

Plants forming rounded clumps, 1.5–2.5 dm tall, from a branching caudex, this clothed with brown to ash colored, marcescent leaf bases, caulescent to apparently subscapose; stems glabrous to scabrous with crisped trichomes; basal leaves 0.5–8 (8.5) cm long, 4–16 mm wide, cuneate to obovate, usually 3- or 4-toothed or -lobed apically, glaucous and hirtellous as well as sparingly long pilose; cauline leaves typically the shorter and wider, cuneate to narrowly obovate, commonly deeply 3-lobed apically and each with an acerose bristle 1–5 mm long; cyme subcorymbose to paniculiform, bracteate; flowers mainly 3–5, on pedicels 2–9 cm long; sepals 2–8 mm long, usually 2, glabrous; petals 4–6, white, 1.5–4 cm long, usually as wide as long, oval to obovate, persistent on and falling with the mature fruit; stamens surpassed by the stigma; anthers 2 mm long, the filaments somewhat dilated; carpels 3 or 5, astylous or the style to 1 mm long; capsules obovoid, 8–13 mm high, 6–9 mm wide, acrocidal along the sutures, splitting ⅓ to ½ the height of the capsule; fruit soon abscissing following dehiscence; seeds shiny black, 2.5–3 mm long, ca. 1.2 mm thick, conspicuously arilate.

This plant is endemic on gypsiferous outcrops of the Moenkopi Formation (primarily the Shnabkaib Member, but also the Middle Red, and Upper Red members) in Washington County, Utah.

The mature capsules, with marcescent petals attached, fall from the plant soon after maturity and serve to aid dispersal by being carried by wind.

As irreplaceable portions of our natural heritage all members of the genus should be regarded a national prize, as jewels of great price, and protected for future generations, whose advocacy this generation must represent. The low bearclaw poppy (*A. humilis*) is being impacted by off-road vehicles and by urban sprawl in the vicinity of St. George. It is legitimately cited as endangered under stipulations of the Endangered Species Act of 1973, as amended. Despite that listing and attempts by concerned federal and state agencies, and many private individuals, the habitat is being systematically impacted by off-road traffic. Only prudent preservation of the habitat will guarantee survival of this species into the future.

Representative specimens: United States. Utah, Washington County, St. George, 23 June 1937, *W. P. Cottam 7238* (BRY!); W side Warner Ridge, 11 April 1983, *E. Neese 12896* (BRY!); 1.5 km E of Bloomington, 1 May 1981, *S. L. Welsh 20388* (BRY!); ca. 5 km S of St. George, 3 May 1970, *S. L. Welsh & N. D. Atwood 9695* (BRY!); S of St. George, 18 May 1971, *L. C. Higgins 4210* (BRY!); Bloomington, Price Hills, 26 May 1983, *L. C. Higgins & B. Welsh 13423* (BRY!).

**Arctomecon californica** Torr. & Frem. *in* Frem. Rep. Expl. Exped. Oreg. & N. Calif. 312. 1845. (Figure 2)

California bearclaw poppy.

Type locality: "This remarkable plant was found in only a single station in the Californian mountains, on the banks of a creek; flowering early in May. The soil was sterile and gravelly. Although very near *Papaver*, it differs so much in habit and in the strophiolate seeds, as well as in other characters that it must be a distinct genus" (Fremont, 1845).

Type: "*Fremont's Expedition to California, 1843–4. No. 429,* May 3, 1844" (NY!) (l.c.).

Plants forming tall to rounded clumps, subscapose, 2.5–6 dm tall, from a branching caudex, this clothed with ash to straw-colored marcescent leaf bases; basal leaves, 5–14 cm long, 3–25 mm wide, cuneate, usually with 3–5 apical teeth each with an acerose bristle 4–10 (12) mm long, hirtellous as well as moderately

Figure 2. Habit sketch of *Arctomecon californica* Torr. & Frem.

long pilose with barbellate trichomes to ca. 10 mm long; stems sparsely pilose and scabrous, glabrous above; pedicels 7–17 cm long; cymes paniculiform, 5- to 20-flowered, 10–30 cm long, with only 1 or 2 foliose bracts, these long pilose; sepals 3, 8–15 mm long, glabrous or sparingly pilose; petals 4 or 6, yellow, 1.5–3.2 cm long, slightly longer than wide; stamens equaling or slightly surpassing the stigma; anthers 2–3 mm long, the filaments filiform; carpels 4 or 5, astylous; capsules ovoid to obconic, 12–23 mm long, 7–10 mm wide, acrocidal along 4 or 5 sutures, splitting not more than ¼ the length of the capsules; seeds shiny black, 2.5–3 mm long, ca. 1.2 mm thick, conspicuously arilate.

The plants occur in gypsic substrates in Clark County, Nevada, and also in Mohave County, Arizona, east of Lake Mead. The populations fluctuate numerically, and often dramatically, in response to rainfall patterns (Meyer, 1987), "disappearing" from sites for several years and reappearing *en masse* (Welsh et al., 1987).

The type of this specimen (LECTOTYPE NY!) consists of a drawing and a fragment envelope containing an immature fruit and portions of a second one. The data on the label are as follows: "Fremont's Expedition to California, 1843–4. No. 429, May 3, 1844. Arctomecon Californicum. *Torr.* 'Specimen lost by Nick Pooley—or the Lithographer. It was the only one collected by Fremont! Found at a place called Las Vegas, near the Rio Virgen in Southern Utah—Lat. 36°10′.'" The drawing has the notation, "(original drawing) by Nick Pooley—Arctomecon californicum." It is evident that Mr. Pooley was one of several artists occasionally employed by Dr. John Torrey in the 1840's to provide illustrations for publication. The surviving illustration shows a plant remarkable for its completeness and beauty, a fact not often in evidence in numerous other Fremont flood-damaged collections from the troubled second expedition (Welsh, 1993). Pooley's illustration will serve as frontispiece in the published version of the work by Welsh (1993) to be published later. The note in Torrey's hand demonstrates a degree of frustration that the specimen was lost. The epithet *californica* denotes the historical designation of the area where the plant was collected, i.e., Alta Californica, then a portion of Mexico (Welsh, 1993). Alta California included not only present California, but Nevada, Utah, Arizona, and portions of Colorado and New Mexico as well. The epithet was well chosen.

Representative specimens: United States. Arizona, vicinity of

Lake Meade, 25 Mar. 1981, *R. K. Gerrisch 4816* (BRY!). Nevada, Clark County, 2 mi. W of Las Vegas, 19 April 1938, *I. W. & C. B. Clokey 8347* (BRY!); 2 mi. S of old town of St. Thomas, W shore of Lake Meade, 4 May 1941, *V. M. Tanner s.n.* (BRY!); do, North of Las Vegas on Hwy 91-93, milepost 38, 4 April 1970, *N. D. Atwood 2387* (BRY!); do, ca. 2 mi. NE of Frenchmans Mt. and ca. 4 mi. NE of Las Vegas, 5 April 1981, *J. C. Stimson 439* (BRY!); do, ca. 18 mi. S of Overton, 21 April 1982, *N. D. Atwood & S. L. Welsh 8605* (BRY!); do, Jct of Cheyenne and Lamb Blvds, Las Vegas, 27 April 1978, *D. Williams s.n.* (BRY!); do, North Las Vegas, Craig Rd., 7 April 1983, *S. L. & S. L. Welsh 21539* (BRY!); do, North-bound lane of I-15, near Nellis Air Force Base, 30 April 1988, *D. Nelson & K. T. Harper 305* (BRY!). Utah, Washington County, Clint Isom Ranch on Coalpits Mesa road, 20 June 1986, *R. B. Warrick 2039* (BRY!).

**Arctomecon merriamii** Coville Proc. Biol. Soc. Wash. 7: 66. 1892.
(Figure 3)

Merriam bearclaw poppy.

Type locality: "Type specimen in the United States National Herbarium, No. 1890, Death Valley Expedition; collected May 1, 1891, a few miles west of Vegas Ranch, Lincoln County, Nevada, by C. Hart Merriam and Vernon Bailey" (l.c.).

Type: "Vegas Valley, Lincoln Co., Nevada, between Cottonwood Cr. & Vegas ranch, *Vernon Bailey 1890,* May 1, 1891" (HOLOTYPE US!; ISOTYPE US!).

Plants clump-forming, 1–4 dm tall, subacaulescent, from a caudex clothed with ash-colored marcescent leaf bases; stems very short; leaves clustered at the base, 3.5–12 cm long, cuneate to obovate, the base cuneate-attenuate, with 3–12 apical teeth (or sometimes merely crenate), each tooth with an acerose bristle 5–12 mm long, moderately to densely long pilose, especially dense near the apex, the trichomes 1–12 mm long, barbellate; inflorescence axis much shortened, cymose, with 1–6 scapose pedicels per stem, these (7) 15–36 cm long; sepals 2–3, 14–20 mm long, pubescent like to the leaves; petals 6, white, 2.5–4 cm long, 2–3 cm wide; anthers 4–5 mm long, the filaments somewhat dilated above; carpels usually 6, astylous; capsule linear-oblong, 2.5–4 cm long, 7–11 mm wide, dehiscing ¼ the length of the capsule along 6 sutures.

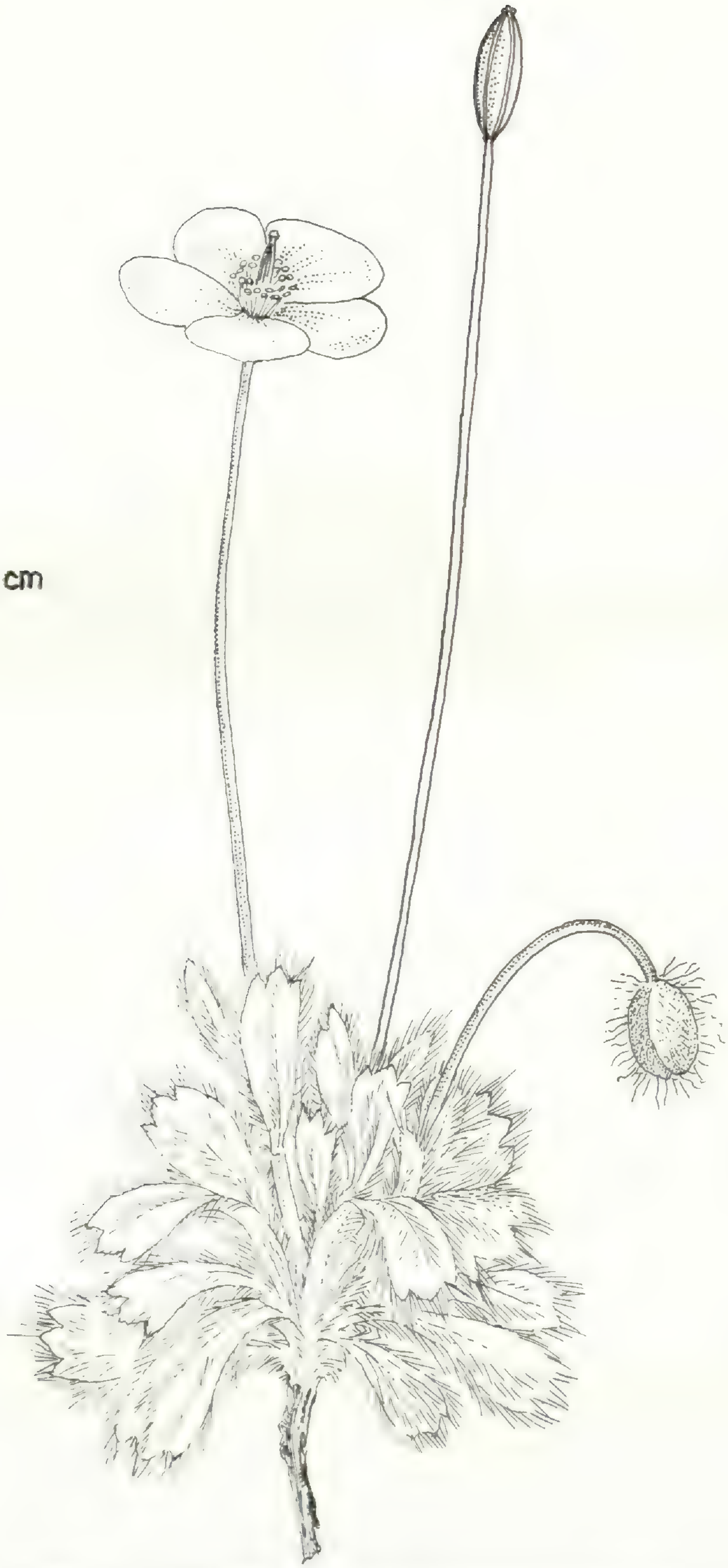


Figure 3. Habit sketch of *Arctomecon merriamii* Coville.

Figure 4. Distribution map for species of *Arctomecon* in southern Nevada and adjacent portions of California and Utah.

This plant grows on gypsic and limestone substrates in Death Valley (Inyo Co., California) and eastward into Nye, Clark, and southern Lincoln counties, Nevada.

The label of the type specimen bears only the name of Vernon

Bailey as collector, but the type is attributed to Merriam, party director, and Bailey. Is it probable that Dr. C. Hart Merriam had no hand in its collection? And, if so, why was it not named for Bailey? There is a hint of playing politics, or of personal distrust or dislike, in the selection of the specific epithet. Coville should have honored collector Bailey with the name.

Representative specimens: United States. California, Inyo County, Racetrack Valley road, ca. 18 km S of Ubehebe crater, 1 April 1982, *Thorne et al. 1595,* 1 April 1982 (BRY!); do, Funeral Mts, road to Chloride, ca. 8 km from Beatty road, 6 April 1983, *K. Thorne & B. Ratcliffe 2342* (BRY). Nevada, Clark County, South of Indian Springs, 26 April 1939, *I. W. Clokey 8238* (BRY!). Lincoln County, Rainbow Canyon road, 10 km E of Hwy 93, 22 April 1988, *D. Nelson 284* (BRY!); do, 10 km E of Hwy 73, along Caliente road, 4 September 1981, *E. Neese & S. Clark 10994* (BRY!); do, Meadow Valley Mts, ca. 23 mi. SW of Elgin, 19 April 1982, *N. D. Atwood & S. L. Welsh 8553* (BRY!).

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# ACHENE MICRO-MORPHOLOGY AS A SYSTEMATIC AID TO THE SERIES PLACEMENT OF SVENSON'S UNDESIGNATED *ELEOCHARIS* (CYPERACEAE) SPECIES

FRANCIS J. MENAPACE[1]

## ABSTRACT

*Eleocharis* species unassigned by Svenson to the series level at the completion of his worldwide monograph were examined utilizing scanning electron microscopy. Acid treated achenes with their cuticle and outer periclinal cell walls removed revealed micro-morphological characters in support of assigning *E. squamigera* and *E. subarticulata* to the series *Palustriformes*, subseries *Truncatae*. Although the results failed to delegate unequivocally *E. albida* and *E. melanocarpa*, additional insight regarding their infrageneric relationship was obtained. An assessment of *E. minarum* proved to be impossible due to the absence of mature achenes.

Key Words: Cyperaceae, *Eleocharis*, micro-morphology, SEM, achene

## INTRODUCTION

The last monographic study of *Eleocharis* R. Br., on a cosmopolitan basis, was conducted by Svenson (1939a). Svenson (1929, 1939a) partitioned *Eleocharis* at the series and subseries levels, based on macro-morphological characters of the culm, floral scales, and fruit, with the achenes being of particular importance. Of the 146 species recognized by Svenson (1939a), five were left unassigned to the series level (*E. albida* Torr., *E. melanocarpa* Torr., *E. minarum* Boeck., *E. squamigera* Svens. and *E. subarticulata* (Nees) Boeck.). Svenson elected to place these plants under the heading "species of uncertain classification" due to the absence or conflicting distribution of diagnostic characters.

Recent survey papers on the micro-morphology of *Eleocharis* achenes found sufficient epidermal characters to warrant their use taxonomically (Varma et al., 1989; Menapace, 1991). A detailed account of achene micro-characters at the series level is provided by Menapace (1991). Such characters as the configuration of the anticlinal cell walls (e.g., entire, crenate, etc.), the contour of the cell lumens (e.g., level, concave, etc.), and the presence or absence of lumen pits and depressions, were found to be systematically

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helpful at the series and subseries ranks. SEM photomicrographs of achenes of representative species were provided in that paper (Menapace, 1991) to illustrate the characters just enumerated.

Given the undesignated series status of the taxa named above, it was of interest to determine if the micro-morphology of their achene walls would add additional features from which to assess their subgeneric relationship.

## MATERIALS AND METHODS

Mature achenes were removed from selected herbarium specimens. In order to evaluate infraspecific variation, two or three collections of each species were examined covering as wide a geographic distribution as possible. Data pertaining to the voucher specimens are provided in Table 1. The cuticle and outer periclinal cell walls of *Eleocharis* achenes obscure systematically pertinent micro-morphological features. As a consequence, these layers must be removed to permit observation of the taxonomically useful characters affiliated with the anticlinal cell walls and cell lumens. The cuticle and outer periclinal cell walls were eliminated by submerging the achenes for 24 hours into a 1:9 concentration of sulfuric acid and acetic anhydride. The achenes were subsequently removed from the acid mixture, sonicated, washed with distilled water, and coated with 30 nm of a gold-palladium alloy utilizing an International Scientific Instruments (ISI) PS2 coating unit. Micrographs were taken solely from the central portion of the achenes with an ISI Alpha-9 Scanning Electron Microscope.

## RESULTS AND DISCUSSION

In a prior study of *Eleocharis* (Menapace, 1991), X-ray spectrometry determined that silicon is the prevailing element of the achene wall, the chemical form of which is believed to be silica.

The initial micrograph (Figure 1) presents an *Eleocharis* achene with the cuticle and outer periclinal cell walls intact. All remaining micrographs, with the exception of Figures 2, 3, and 11, are *Eleocharis* achenes in which the cuticle and outer periclinal cell walls have been removed to reveal features of the anticlinal cell walls and cell lumens.

Table 1. Collection data of specimens utilized for SEM observations.

*Eleocharis acicularis.* UNITED STATES. **Illinois:** Jackson Co., Elkville, *Mohlenbrock 5760* (SIU); **Nebraska:** Lincoln Co., Kings Lake, *Kellogg s.n.* (SIU); **Maine:** Knopp Co., Razorville, *Steyermark 712* (MO).

*Eleocharis albida.* BERMUDA. **Pembroke Parish:** Pembroke Marsh, *Moore 3164* (GH); MEXICO. **Tamaulipas:** Tampico, *Palmer 570* (GH); UNITED STATES: **Florida:** Levy Co., Waccasassa Bay, *Easterday s.n.* (FSU).

*Eleocharis elegans.* CUBA. **Oriente:** La Carmit Florida Blanca, *Clements 1990* (GH); ECUADOR. **Guayas:** Tenquel, *Holmgren 99* (S); JAMAICA. **St. Anne:** Frazer, *Proctor 34808* (IJ).

*Eleocharis elliptica.* UNITED STATES. **Michigan:** Charlevoix Co., Beaver Island, *Menapace, 24* (SIU); Beaver Island, *Menapace 25* (SIU).

*Eleocharis filiculmis.* BELIZE. **Cayo:** San Luis, *Dwyer 338* (SIU); DOMINICAN REPUBLIC. **Trujillo:** Bayaquana, *Alain 22448* (GH); HONDURAS. **Morazan:** Las Mesas, *Williams 17054* (WIS).

*Eleocharis geniculata.* JAMAICA. **Manchester:** Cut River, *Proctor 35384* (IJ); PERU. **Loreto:** Pongode Manseriche, *Mexia 6174* (GH); UNITED STATES. **Florida:** Gulf Co., White City, *Godfrey 75703* (FSU).

*Eleocharis intermedia.* CANADA. **Ontario:** Renfrow Co., Lyndoch Township, *Dickson 1413* (CAN); UNITED STATES. **Indiana:** Nobel Co., Blackman Lake, *Deam 21865* (IND); **Massachusetts:** Berkshire Co., Pontoosue Lake, *Churchill s.n.* (MO).

*Eleocharis melanocarpa.* UNITED STATES. **Indiana:** Porter Co., Indiana Dunes St. Park, *Umbach 3817* (MO); **Texas:** Leon Co., Oakwood, *Palmer 13404* (MO); **Massachusetts:** Barnstable Co., Osterville, *Proctor 38072* (IR).

*Eleocharis multicaulis.* FRANCE. **Allier:** *Chassignol 903* (NY); PORTUGAL. **Azores:** Terceira Island, *Silva 135* (NY); SWEDEN. **Blekinge:** Ronneby, *Broddeson 2* (NY).

*Eleocharis nodulosa.* GUATEMALA. **El Quiche:** Nabaj, *Proctor 25301* (IJ); HONDURAS: **Comayagua:** Siguatepeque, *Errazuriz 112* (SIU); **Morazan:** La Venta, *Espinosa 168* (SIU).

*Eleocharis pachystyla.* COSTA RICA. **Puntarenas:** *Davidse 1269* (MO); CUBA. **Moa:** Oriente, *Clements 3588* (GH).

*Eleocharis parvula.* UNITED STATES. **Florida:** Collier Co., Marco, *Kattato 749* (SIU).

*Eleocharis quinqueflora.* CANADA. **Saskatchewan:** Cypress Hills, *Breitung 5178* (MO); UNITED STATES. **Illinois:** McHenry Co., Ringwood, *Vassey s.n.* (SIU); **Michigan:** Charlevoix Co., Beaver Island, *Menapace 87* (SIU).

*Eleocharis pellucida.* JAPAN **Honshu:** *Togasi 1103* (NY); Nara City, *Kitagawa 307* (NY); **Kyushu:** Lake Odako, *Koyama 7012* (NY).

*Eleocharis rostellata.* UNITED STATES. **Arizona:** Santa Cruz Co., Canelo Hills Nature Preserve, *Adams s.n.* (SIU); **New Jersey:** Ocean Co., Barnegat Bay, *Hermann 4392* (MO).

*Eleocharis squamigera.* BRAZIL. **Parana:** Jaguariaiva, *Dusen 13276* (NY); **Santa Catarina:** Campo Ere, *Smith 13673* (NY); Cacador, *Smith 8982* (NY).

*Eleocharis subarticulata.* BRAZIL. *Gardner 719* (MO); **Santa Catarina:** Cacador, *Smith 8990* (NY); **Parana:** Curitiba, *Dusen 116a* (NY).

*Eleocharis tenuis.* UNITED STATES. **New Jersey:** Ocean Co., Lanoka Harbor, *Hirt 1387* (NY); Cape May Co., Villas, *Wilson 910* (NY); **New York:** Suffolk Co., *Cambell 163* (GH).

In the discussion that follows the "species of uncertain classification" are assessed in accordance with the micro-morphological characters of the achene wall.

**Eleocharis albida** Torr.

*Eleocharis albida* is a North American maritime spikerush from Maryland to central Mexico (Gleason, 1952). In his initial review of *Eleocharis,* Svenson (1929) assigned *E. albida* to the series *Sulcatae*, only to describe it at the completion of his study as a plant of ". . . unknown affinity . . .," a species not allied to any other *Eleocharis* (Svenson, 1939a). In his final monographic work, covering North American *Eleocharis,* Svenson (1957) suggested that *E. albida* may be allied to the series *Pauciflorae,* although a detailed justification was not provided.

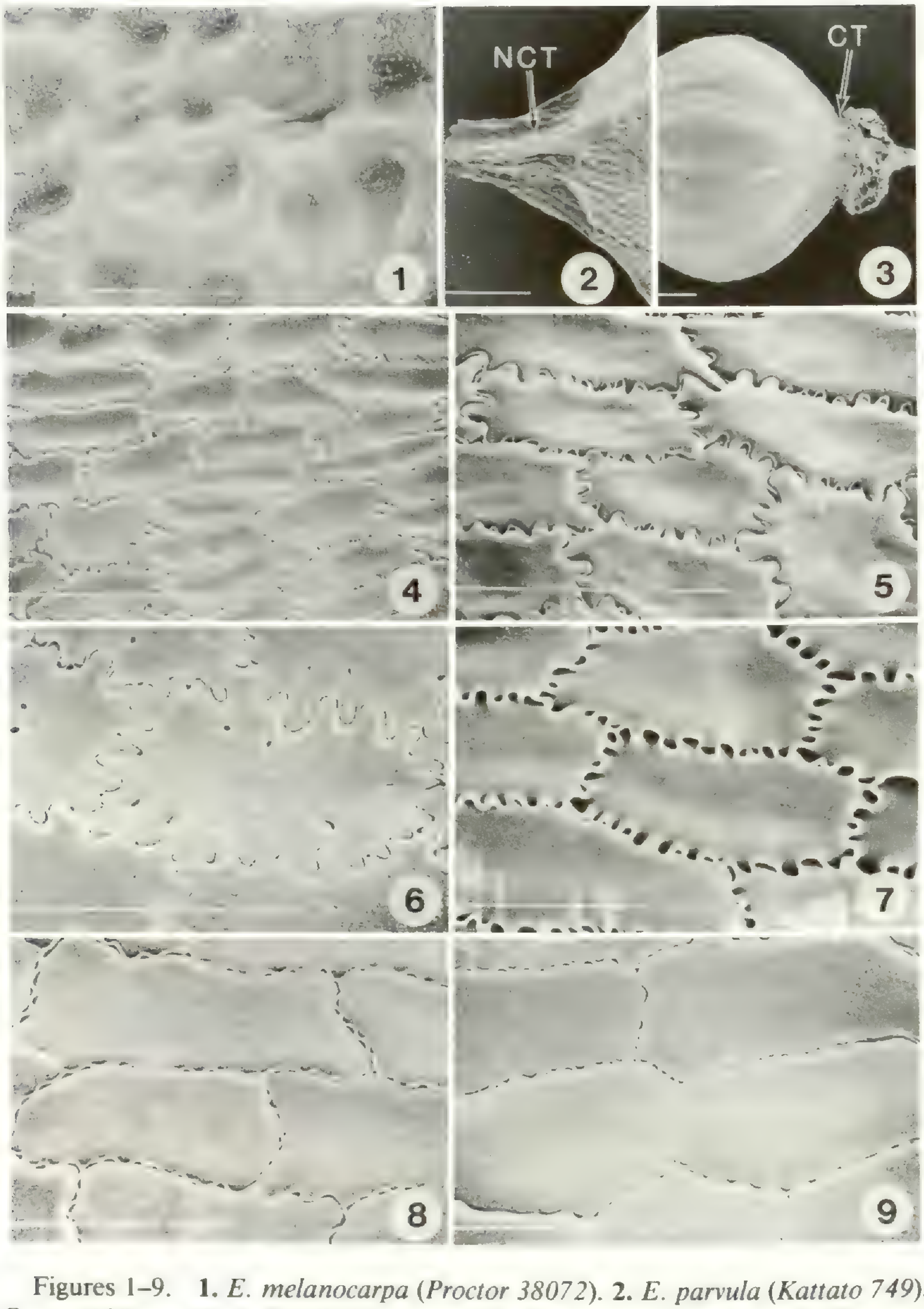
Plants of the *Pauciflorae* possess trigonous achenes that lack a constricted tubercle (e.g., *E. parvula* (R. & S.) Link, Figure 2, NCT). The fruit of *E. albida* is in fact trigonous, however, a large constricted tubercle is also present (Figure 3, CT). There is little question that the constricted condition of the tubercle persuaded Svenson to refrain from formally assigning *E. albida* to the *Pauciflorae.*

On a micro-morphological basis, the achenes of *E. albida* (Figures 4 and 5) bear widely crenate to dentate anticlinal cell walls, with undulating to level lumens that are rarely pitted. Attributes of this nature suggest a relationship with *E. filiculmis* Kunth series *Sulcatae* (Figure 6), *E. multicaulis* (Smith) Smith series *Multicaules* (Figure 7), *E. pellucida* Presl series *Multicaules* (Figure 8), and *E. pachystyla* (Wright) C. B. Clarke series *Sulcatae* (Figure 9).

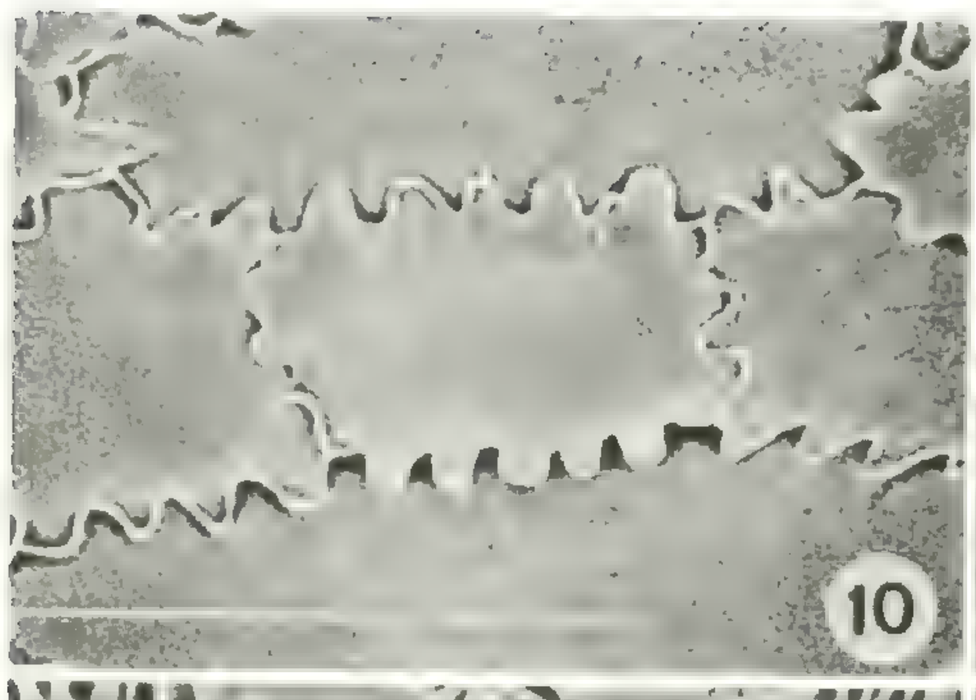
The anticlinal cell walls of *E. geniculata* (L.) R. & S. (Figure 10), series *Maculosae,* are also crenate to dentate. However, in contrast to the trigonous achenes of *E. albida,* the achenes of *E. geniculata* are lenticular. Such a salient difference is sufficient, in the author's judgement, to preclude a close affiliation between *E. geniculata* and *E. albida.*

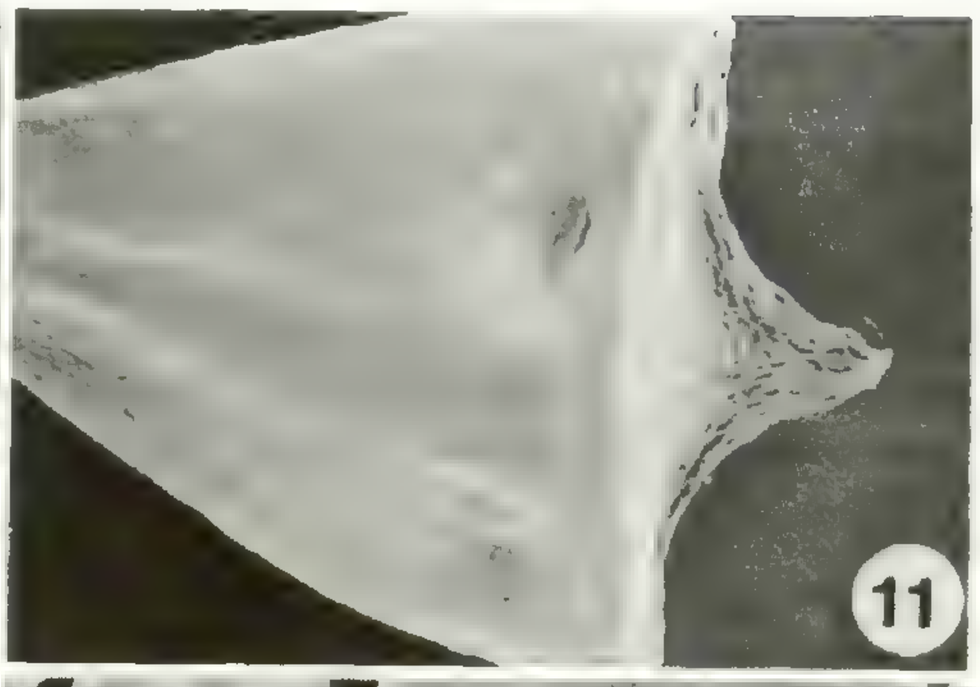
**Eleocharis melanocarpa** Torr.

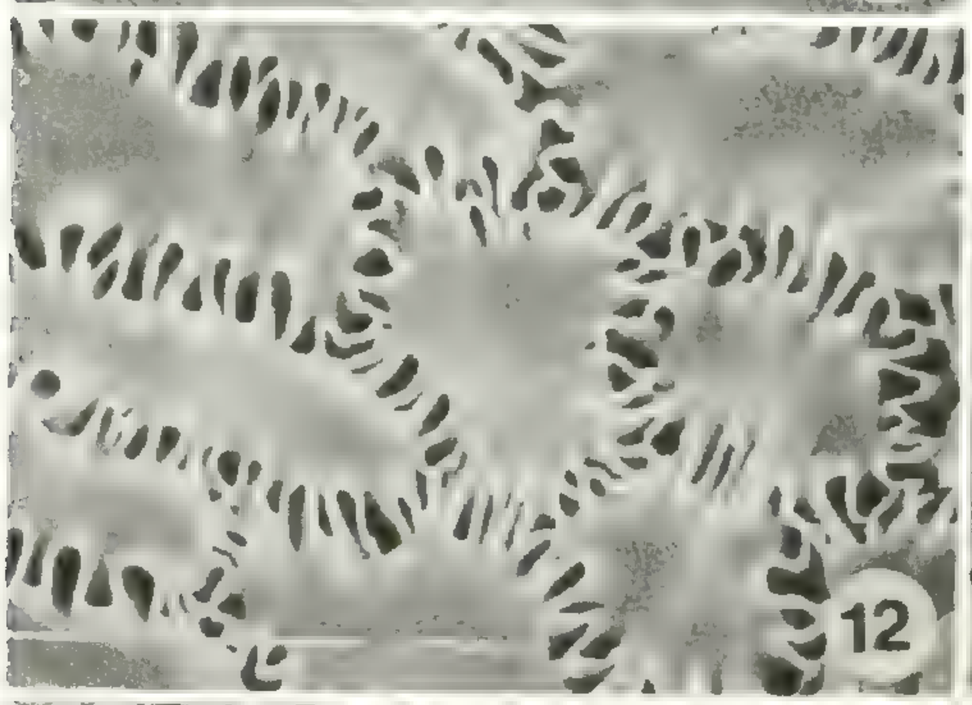
Although encountered sporadically within the interior of North America, *E. melanocarpa* is primarily a sedge of the Atlantic coastal plain from Massachusetts to Texas (Gleason, 1952). Sven-

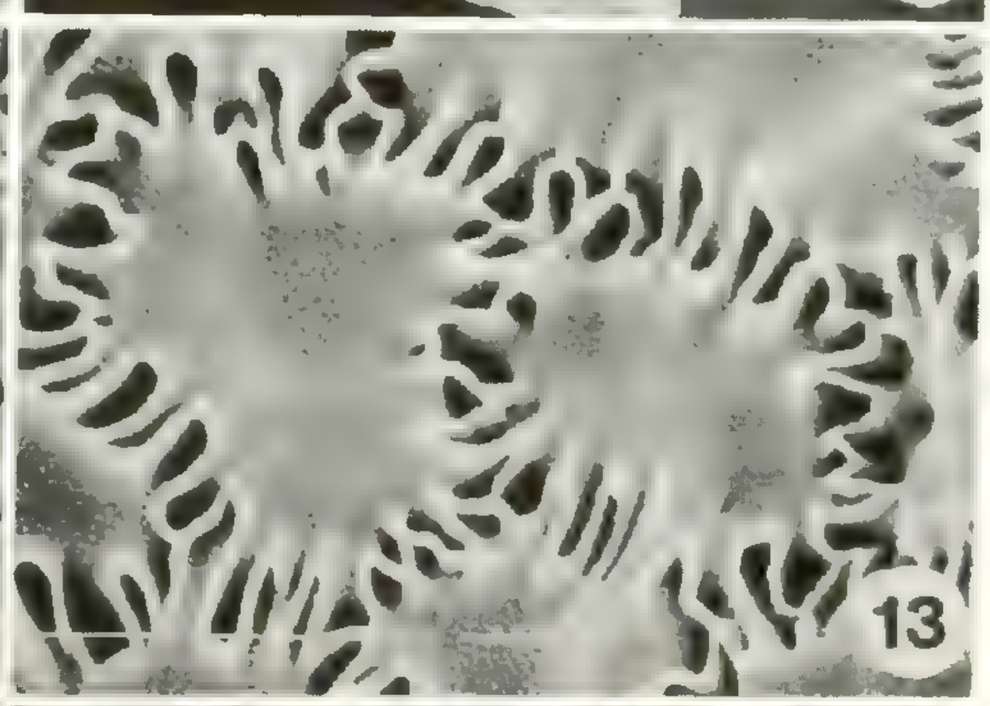


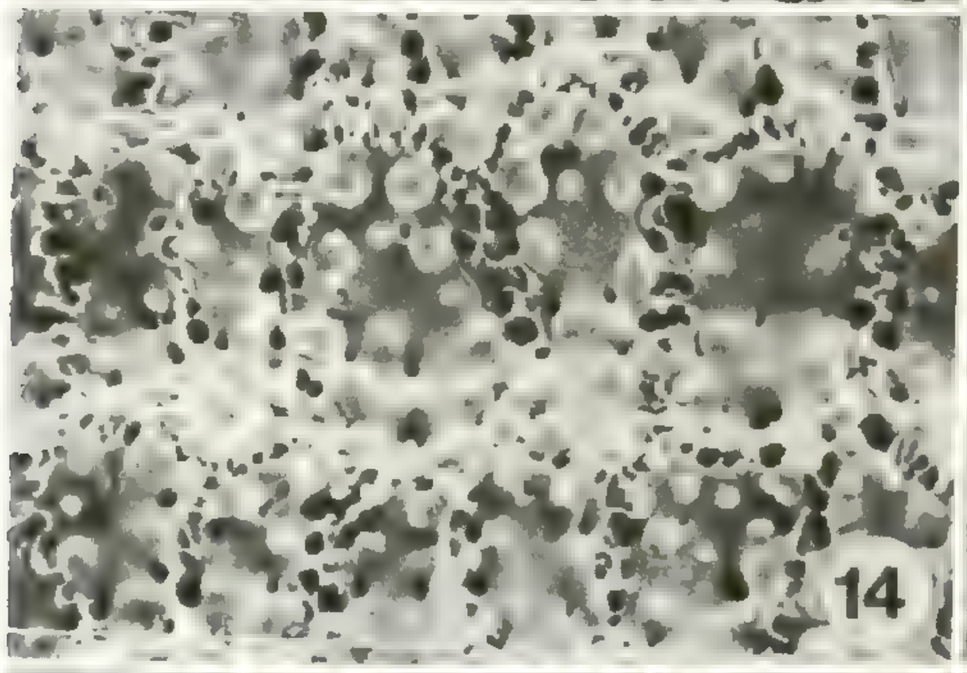

Figures 1–9. **1.** *E. melanocarpa* (*Proctor 38072*). **2.** *E. parvula* (*Kattato 749*), Bar = 100 μm. **3–5.** *E. albida* (*Moore 3164*), Bar = 100 μm. **6.** *E. filiculmis* (*Williams 17054*). **7.** *E. multicaulis* (*Silva 135*). **8.** *E. pachystyla* (*Clements 3588*). **9.** *E. pellucida* (*Koyama 7012*). Gap in bars = 1 μm. NCT = non-constricted tubercle, CT = constricted tubercle.

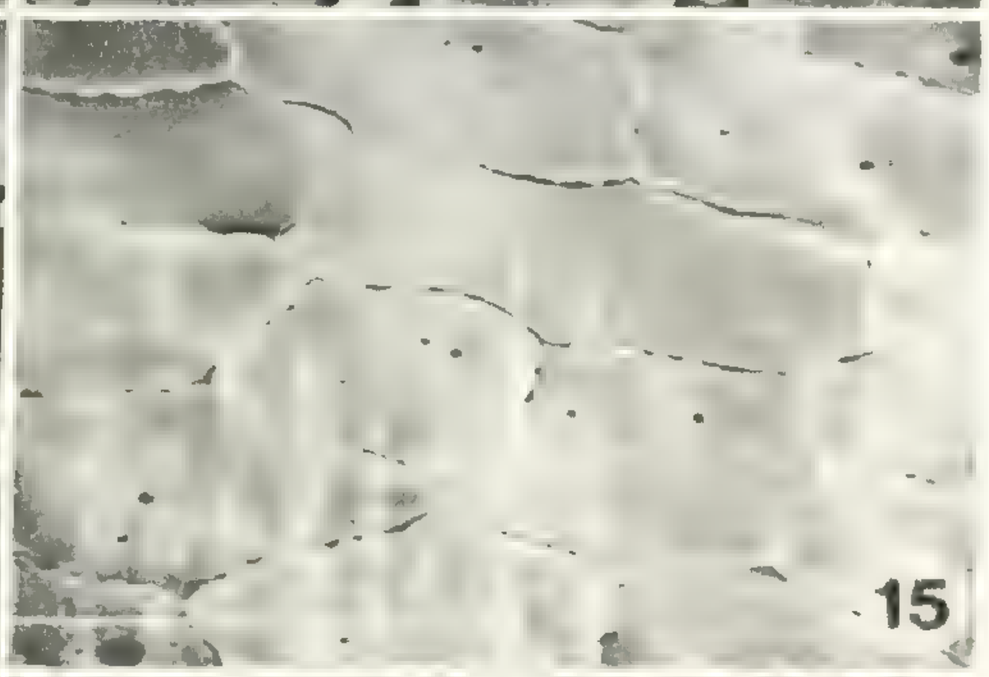


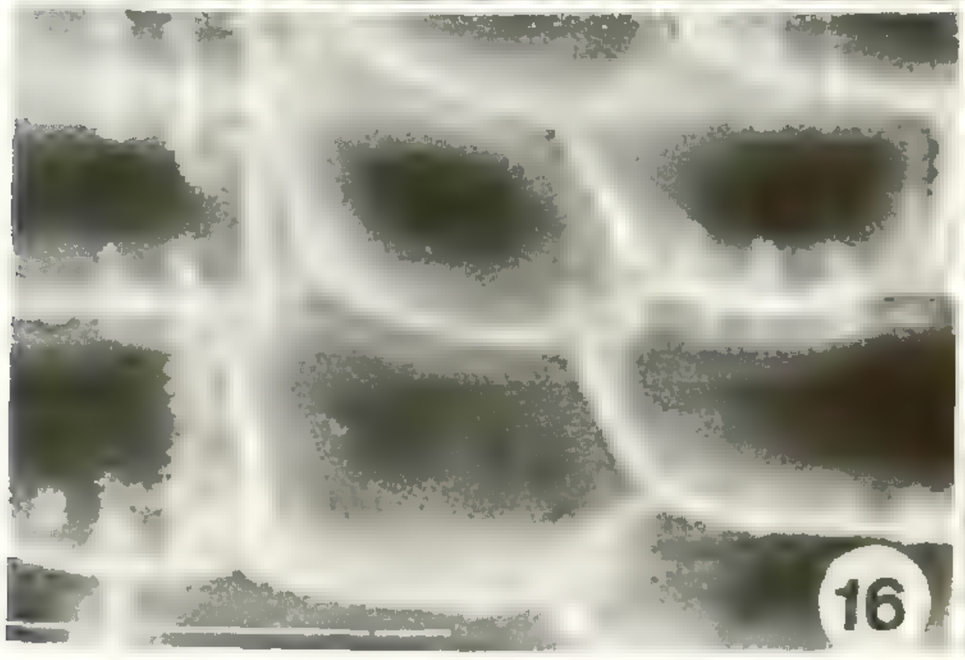



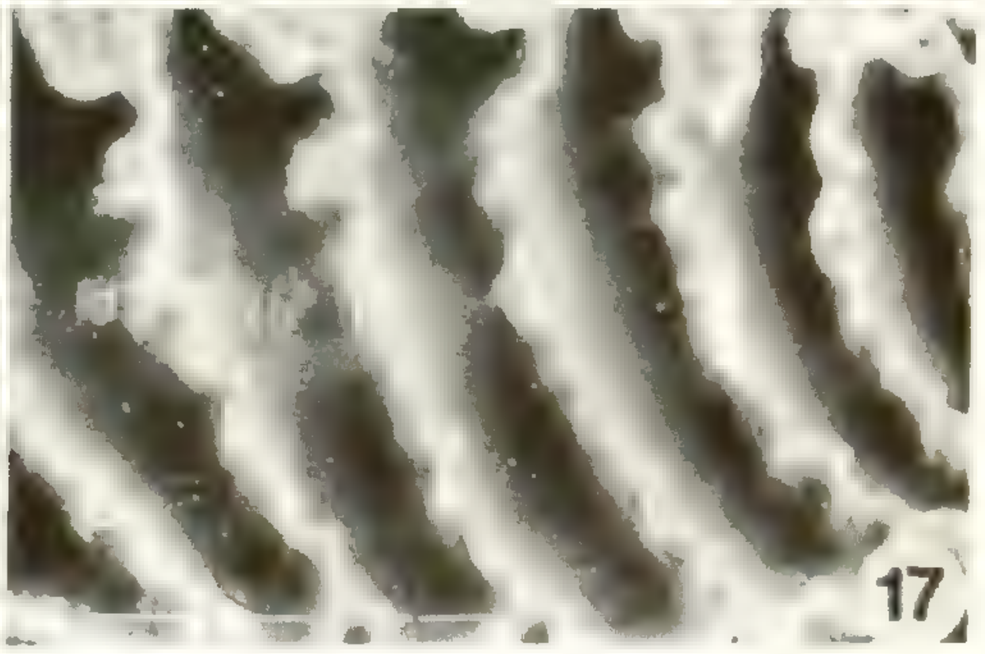




Figures 10–17. **10.** *E. geniculata* (*Godfrey 75703*). **11–13.** *E. melanocarpa* (*Proctor 38072*), **14.** *E. quinquefolia* (*Menapace 87*). **15.** *E. rostellata* (*Hermann 4392*). **16.** *E. tenuis* (*Hirt 1387*). **17.** *E. acicularis* (*Mohlenbrock 5760*). Gap in bars = 1 μm.

son (1929), initially assigned *E. melanocarpa* to its own monotypic series, the *Melanocarpeae*. At the completion of his monographic study, however, Svenson (1939a) abandoned the *Melanocarpeae* relegating *E. melanocarpa* to uncertain status.

Later, Svenson (1957) again modified his view and formally delegated *E. melanocarpa* to the series *Pauciflorae,* although a detailed explanation regarding this assessment was not given.

As previously noted, the tubercles of *Pauciflorae* achenes are confluent with the achene body (Figure 2). There is little doubt that the highly appressed, non-constricted tubercle of *E. melanocarpa* (Figure 11) was a key factor in Svenson's decision to allocate *E. melanocarpa* to the *Pauciflorae.* Although the convolute anticlinal cell walls of *E. melanocarpa* (Figures 12 and 13) do not repudiate Svenson's decision to assign *E. melanocarpa* to the *Pauciflorae*, given the absence of achene conformity at the micro-morphological level within the *Pauciflorae* (e.g., *E. quinqueflora* (F. X. Hartm.) O. Schwarz, Figure 14, and *E. rostellata* Torr., Figure 15), the author questions whether the series, is in fact, a natural entity.

Similar to *E. albida,* the convolute anticlinal cell walls of *E. melanocarpa* implies a relationship with either the *Multicaules* or *Sulcatae.*

**Eleocharis minarum** Boeck.

*Eleocharis minarum* is a taxon of questioned authenticity. Svenson (1939b), after examining the syntypes deposited at Stockholm (S) and Copenhagen (C), discovered that *E. minarum* was based on immature plants, possibly allied to *E. dunensis* Kuek. of the series *Sulcatae.* The author has also inspected the Stockholm and Copenhagen plants, and concurs with Svenson's assessment.

A thorough search of the world's major herbaria failed to secure a mature specimen of *E. minarum.* Given the absence of a plant bearing mature achenes, a micro-morphological evaluation was not possible.

**Eleocharis squamigera** Svens.

This species is a South American spikerush about which little has been published. *Eleocharis squamigera* has been collected from scattered localities throughout the tropical regions of the continent (Svenson, 1934).

According to Svenson (1934), the general morphological appearance of *E. squamigera* is similar to *E. tenuis* Schult., of the

series *Palustriformes* subseries *Truncatae.* In fact, the type specimens of *E. squamigera* were initially assigned to *E. tenuis* (Svenson, 1934). Nonetheless, the micro-morphology of the achenes differ in that the anticlinal cell walls of *E. squamigera* (Figures 18 and 19) are crenate to serrate, while those of *E. tenuis* (Figure 16) are serrulate to entire. Furthermore, the cell lumens of *E. tenuis* are more concave than those of *E. squamigera.* Clearly, the two plants are distinct, allied taxa.

Svenson (1934) also suggested an affinity with the series *Aciculares.* However, achenes of the *Aciculares* possess highly elevated anticlinal cell walls (e.g., *E. acicularis* (L.) R. & S., Figure 17), a feature which is lacking from the achenes of *E. squamigera.*

Although the achene micro-morphology of *E. squamigera* contrasts somewhat with that of *E. tenuis,* it does approximate other taxa of the series *Palustriformes* subseries *Truncatae* (e.g., *E. nodulosa* (Roth) Schult., Figure 20, and *E. intermedia* (Muhl.) Schult., Figure 21).

**Eleocharis subarticulata** (Nees) Boeck.

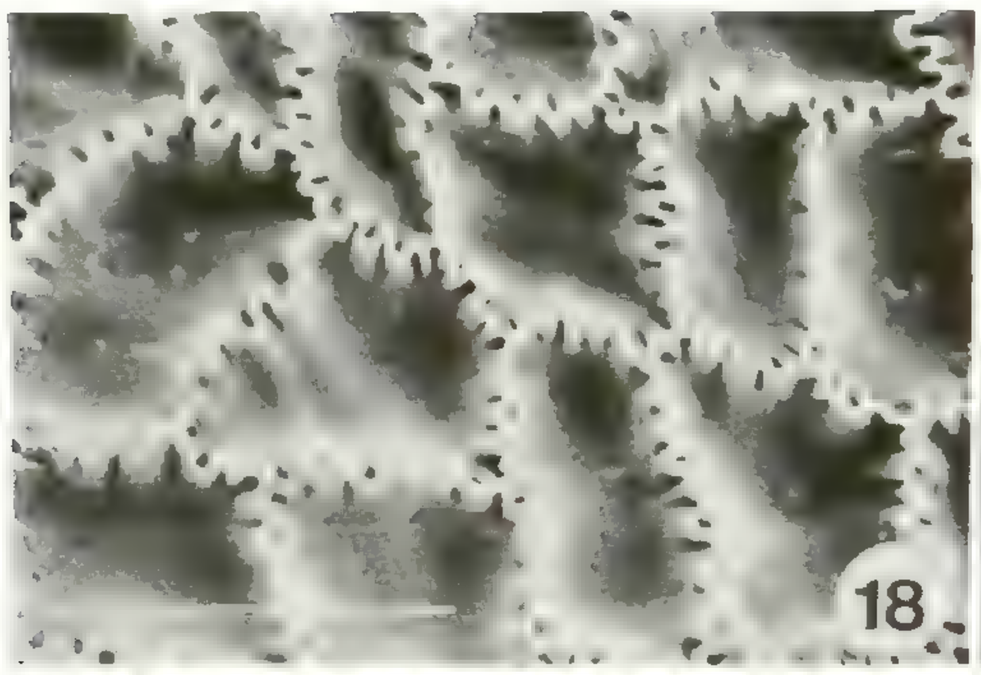
*Eleocharis subarticulata,* like much of the spikerush flora of Latin America, suffers from a lack of modern studies. Svenson (1939b) found the vegetative and achene characters to be near *E. intermedia,* a plant of the series *Palustriformes* subseries *Truncatae* of North American distribution.

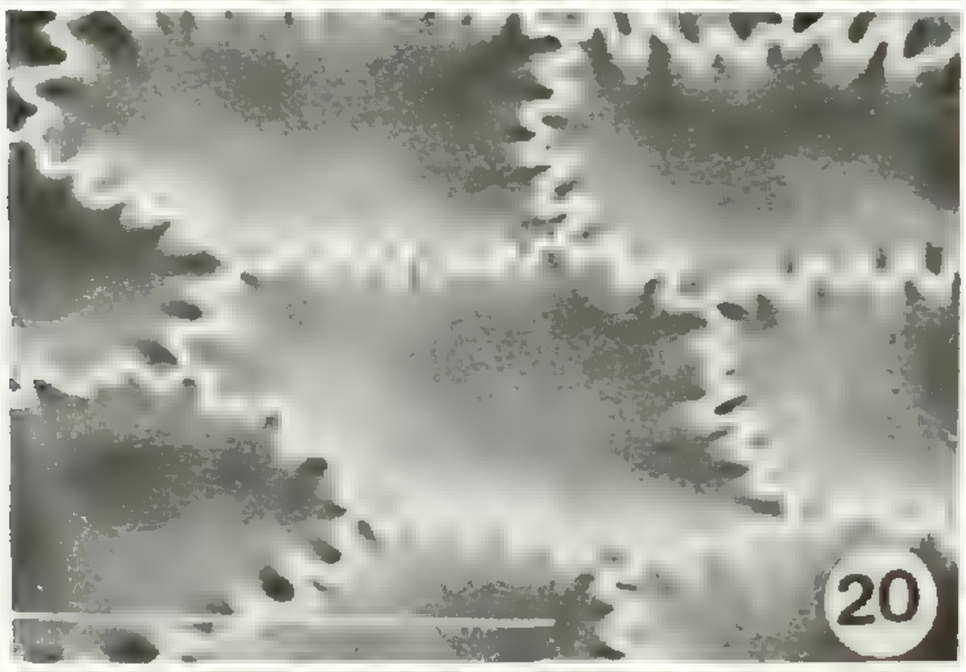
The micro-morphology of the achene wall (Figures 22 and 23) also suggests an alliance with the *Truncatae.* The anticlinal cell walls are repand to crenate with slightly concave lumens, attributes which are consistent in outline with *E. elegans* (H.B.K.) R. & S. (Figure 24) and to a lesser extent with *E. elliptica* Kunth (Figure 25).

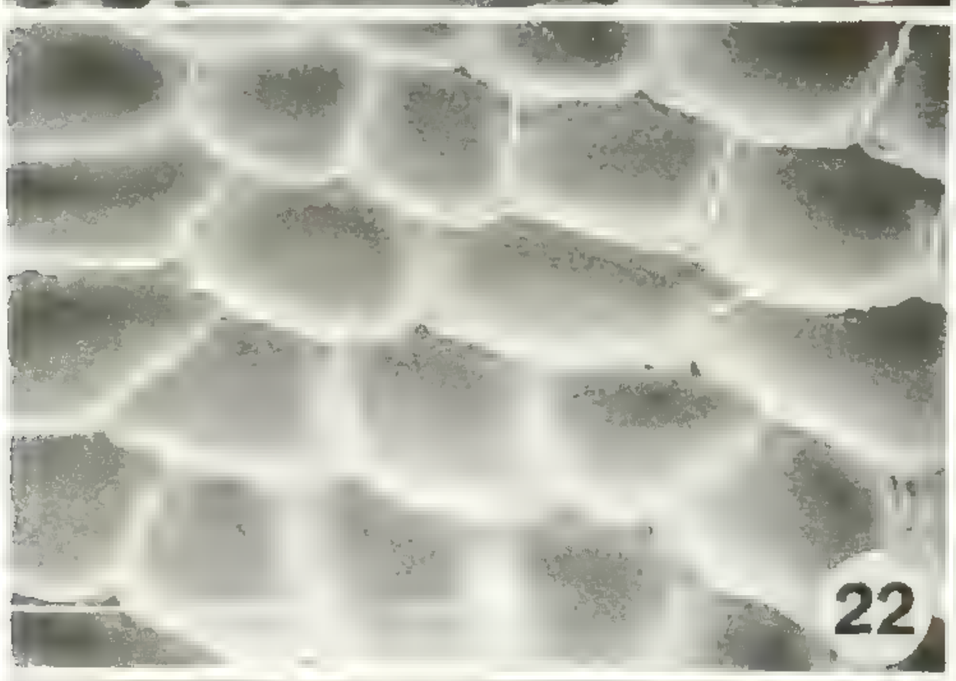
## SUMMARY

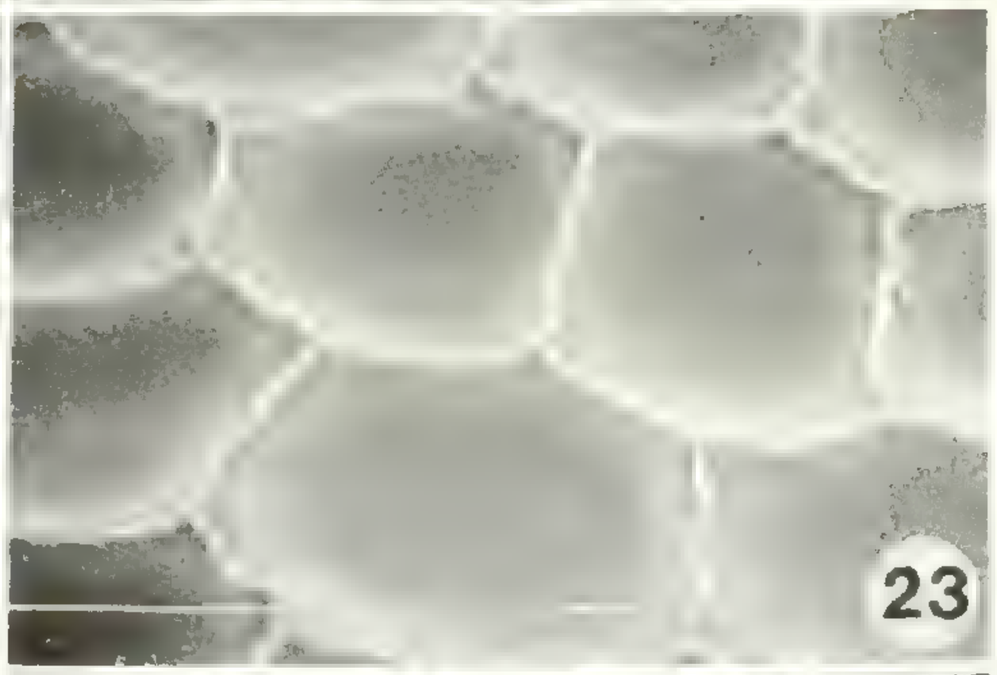
Micro-morphological characters of the achene wall add credence to Svenson's (1929) conclusion that *E. albida* is allied to the series *Sulcatae.* The results are equally conducive, however, to a relationship with the series *Multicaules.* Consequently, a definitive decision regarding the serial placement of *E. albida* was not obtained.

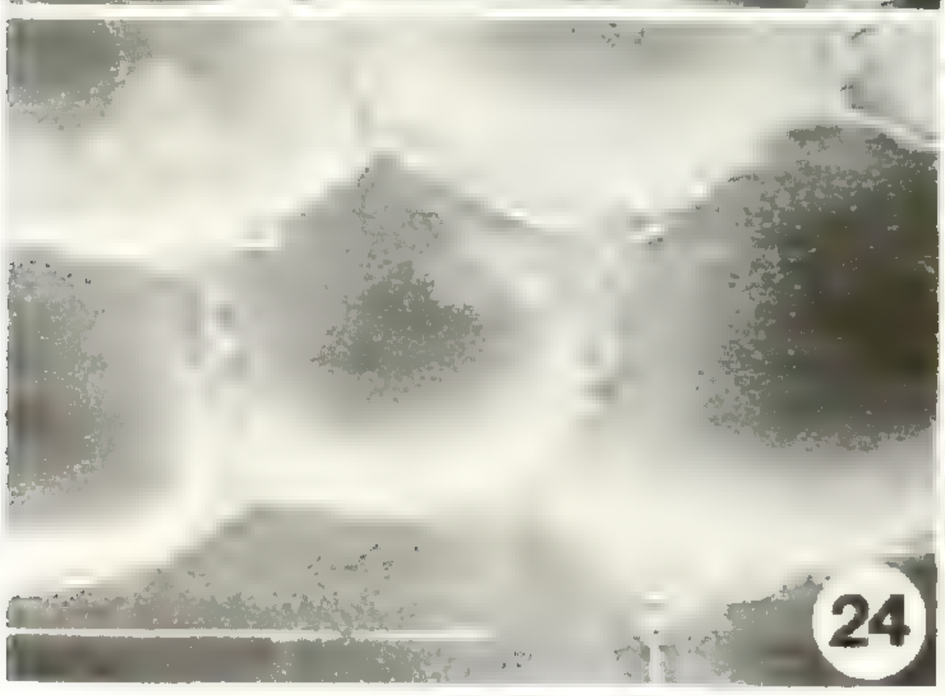
The micro-morphological attributes affiliated with the achenes







Figures 18–25. **18** and **19.** *E. squamigera* (*Smith 13673*). **20.** *E. elegans* (*Proctor 34808*). **21.** *E. intermedia* (*Dickson 1413*). **22** and **23.** *E. subarticulata* (*Smith 13673*). **24.** *E. nodulosa* (*Proctor 25301*). **25.** *E. elliptica* (*Menapace 24*). Gaps in bar = 1 μm.

of *E. melanocarpa* were also inconclusive. The convolute anticlinal cell walls suggest a kinship with either the *Multicaules* or *Sulcatae.* Nonetheless, the evidence is once again equivocal as to which series is in fact the best alternative.

Given the continued ambiguity surrounding the serial placement of *E. albida* and *E. melanocarpa,* it is considered best to retain their status as "species of uncertain classification."

With regard to *E. squamigera* and *E. subarticulata,* the author has concluded that the achene micro-morphology constitutes sufficient evidence, in conjunction with the overall macro-morphological affinities, to assign *E. squamigera* and *E. subarticulata* to the series *Palustriformes* subseries *Truncatae.*

An assessment of *E. minarum* proved to be impossible due to the absence of a specimen bearing mature achenes.

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# REDISCOVERY OF THE MANY-CROWNED STRAWBERRY, *FRAGARIA MULTICIPITA* FERNALD

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**ABSTRACT**

Three stations of *Fragaria multicipita* Fernald were rediscovered in the general area of the type locality along Rivière Ste.-Anne in Gaspé, Québec. This taxon has not been accepted as a species by a number of recent compilers and monographers, but the plants retained distinctive features under greenhouse cultivation suggesting that taxonomic recognition may be appropriate, although the appropriate rank is unclear. The distinctive features include small size, small almost stalkless leaflets and a multicipital, more or less runnerless caudex. The plants were confined to dry sandy or silty, open riverine bars. Study of living plants of *F. multicipita* may help to further elucidate the nature of endemism in northeastern North America. It will also contribute additional information relevant to the classification of strawberries, this in turn providing the information needed for optimal germplasm protection and for increasing the low genetic diversity of strawberries cultivated in North America. Where *F. multicipita* occurs there is substantial variation in native species of *Fragaria,* and *in situ* as well as *ex situ* protection is desirable.

Key Words: *Fragaria multicipita,* strawberry, distribution, ecology, taxonomy, phytogeography, endemism, Gulf of St. Lawrence, germplasm protection, Québec, Canada

*Fragaria multicipita* was described by M. L. Fernald in 1908 on the basis of material that he collected with J. F. Collins (*230,* GH) along Rivière Ste.-Anne in Gaspé, Québec. The species was never discovered anywhere else and Fernald was unable to relocate the plants in 1927 when he found that the type locality had been used for a logging camp and the habitat there completely destroyed (Fernald, 1940). Many botanists visited the Ste.-Anne valley to search for *Fragaria multicipita,* but all searches were unsuccessful and it was assumed to be extinct (Drury, 1969; Scoggan, 1978). Having been known only from the type collection for 84 years, it was rediscovered in 1992 at three separate localities along the Rivière Ste.-Anne. Pressed specimens of recently collected plants have been deposited at DAO and MT and living material is being propagated for further research. The purposes of the following notes are to outline the history of this taxon, and to provide some new information resulting from its rediscovery, along with an indication of its potential significance.

## TAXONOMIC HISTORY

*Fragaria multicipita* was retained as a species by Rydberg (1908) in his monograph produced the same year that Fernald described the plant. It was one of three species of strawberries recognized in northeastern North America by Fernald in 1950, and it was accepted by Scoggan the same year in his flora of Bic and the Gaspé Peninsula.

Most authors after 1950 either overlooked it, rejected it entirely, or placed it in synonymy under *F. virginiana* with neither explanation nor comment. Among the reasons for this are the two facts that it was not found again (see above) and that the most influential botanists concerned with northeastern North America at the time were "lumpers" who considered taxa described by Fernald as the products of extreme splitting. Gleason (1952) placed *F. multicipita* in synonymy under *F. virginiana* var. *terrae-novae* (Rydb.) Fern. & Wieg. *Fragaria multicipita* was not mentioned by Boivin (1966) or Gleason and Cronquist (1963, 1991). Staudt (1962) in a monographic work on *Fragaria* did not mention *F. multicipita,* nor was it mentioned by him (1989) in a recent synopsis of the species of *Fragaria.* Scoggan (1978) rejected *F. multicipita* from the flora of Canada. but he nevertheless discussed it in some depth. He correctly noted that Staudt (1962) had treated plants of *F. vesca* from Europe that were without runners as f. *eflagellaris* (Dcne.) Staudt, although he (Staudt) had not mentioned *F. multicipita.* Kartesz and Kartesz (1980) treated *F. multicipita* as a synonym of *F. virginiana* ssp. *virginiana.* With this lack of acceptance it is not surprising that it was not mentioned in recent listings of the rare plants of Québec (Bouchard et al., 1983; Lavoie, 1992).

Regardless of a recent lack of acceptance, *F. multicipita* has not been lost completely. Rice et al. (1982) listed it as one of four species of *Fragaria* occurring in Canada and the United States. A number of recent studies have found Fernaldian taxa to be discrete and worthy of recognition. Among these are studies of other northeastern endemic species named by Fernald such as *Aster anticostensis* Fernald and *Aster laurentianus* Fernald, both of which have recently proved worthy of species rank (Brouillet and Labrecque, 1987; Houle and Haber, 1990; Labrecque and Brouillet, 1990). Despite taxonomic recognition of some aberrations and an untenable varietal concept, taxa described by Fer-

nald are now more widely regarded as the potentially astute observations of one of North America's great taxonomists. As noted by Drury (1969); "Fernald's judgement and ability to separate cogent from trivial differences were amazing."

## DISTINCTIVE FEATURES

Although Fernald (1908) described the plant as caespitose with the caudex divided into several to many crowded upright branches that were very rarely stoloniferous, and he named it *multicipita* in reference to the multicipital caudex (i.e., the root top or stem base with many crowns or heads), it was not until 1950 in the 8th edition of Gray's manual that it became completely clear that this is what he regarded as one of the most distinctive characters. Additionally Fernald (1950) used the relatively small leaves (less than 3 cm long) with sessile leaflets possessed by *F. multicipita* to distinguish it from *F. virginiana.*

Rydberg (1908) also used the lack of runners and the small sessile leaflets to distinguish *F. multicipita* from other species, but he also employed its short petals less than 5 mm long to distinguish it from his *Fragaria terrae-novae* Rydb., which most subsequent authors placed with *F. virginiana,* either as a synonym or as a variety (e.g., Fernald, 1950). Scoggan (1950) utilized Rydberg's (1908) key characters in his flora of Bic and the Gaspé Peninsula. *Fragaria multicipita* was basically distinguished as a small-leaved bushy strawberry lacking runners (Figure 1) by those taxonomists who recognized it.

## REDISCOVERY AND RECENT OBSERVATIONS

Much of the lower valley of Rivière Ste.-Anne is a broad and more or less flat floodplain. Although the river is relatively fast flowing, it meanders through riverine deposits of gravel, sand and silt. The disturbance and erosion from periodic torrential flooding accompanied by ice-scouring in spring, and later deposition results in extensive open areas near the river. Substrates vary in amounts of disturbance as well as composition and wetness, the latter a consequence of height and slope. Although some of the deposits are without vegetation cover, where disturbance is limited or deposition less recent, a vegetation cover has developed. *Fragaria multicipita* was rediscovered on dry, open, gentle slopes

Figure 1. The holotype of *F. multicipita* (Fernald & Collins 230, GH).

on bars composed of silt, fine sand, or gravel (Figure 2) where few other plants occurred and the vegetation cover was sparse. At 4 km SSE of Ste.-Anne-des Monts, 20 plants were found. At approx. 9 km SSE of Ste.-Anne-des-Monts, 52 plants were found.

Figure 2. A, Rivière Ste.-Anne, Gaspé, showing extensive open, silty sandy and gravel bars where *Fragaria multicipita* still occurs. The habitat extends across the center of the photograph between the barren, rocky rivershore and the encroaching forest.

At approx. 13 km SSE of Ste.-Anne-des-Monts, 15 plants were found. Ten of the plants found at the station 9 km SSE, growing on an isolated bar differed from the type material only in having spreading instead of appressed trichomes on the leaf petioles.

Other species growing with or near to *Fragaria multicipita* included *Achillea millefolium* L. ssp. *borealis* (Bong.) Breitung, *Bromus ciliatus* L., *B. inermis* Leyss., *Chrysanthemum leucanthemum* L., *Dryas drummondii* Richards., infrataxa of *Elymus trachycaulus* (Link) Gould in Shinn., *Elytrigia repens* (L.) Nevski, *Fragaria virginiana* Miller, *Galium mollugo* L., *Oenothera parviflora* L., *Poa compressa* L., *P. pratensis* L., *Rubus pubescens* Raf. and *Silene vulgaris* (Moench) Garcke.

The variation in *Fragaria* along Rivière Ste.-Anne is remarkable. In addition to *F. multicipita* with either spreading or appressed trichomes, *F. vesca* L. ssp. *americana* (Porter) Staudt occurs in moist and more shaded places. Finally, plants referable to *F. virginiana* Miller but of different heights, had divergent or

appressed ascending trichomes on the petioles, large or small leaflets of various shapes and numbers with long or short petioles, and stolons of various lengths, colors and thicknesses. One obvious potential explanation for the variation is the remarkable range of adjacent habitats, but a mingling of glacial and preglacial relicts (Drury, 1969; Fernald, 1925) with more recent invaders is also a possibility.

The Ste.-Anne rivershore environment includes some interesting subarctic or alpine elements, in addition to *Dryas drummondii,* such as *Carex atratiformis* Britton, *C. capillaris* L., and *C. media* R. Br. These elements present a striking contrast to the surrounding forest and are only a few of the species included in the distinct and restricted rivershore flora of the region (Labrecque and Brouillet, 1990; Scoggan, 1950). Some of these elements, such as the arctic and cordilleran *Lathyrus venosus* Muhl. var. *intonsus* Butters & St. John, are known from only one, or a very few, eastern stations. Other well established northeastern endemics, such as *Aster anticostensis* Fernald and *Pedicularis furbishiae* S. Watson, are also species of disturbed rivershores. The Gaspé Peninsula and the general region of the Gulf of St. Lawrence have been identified as an evolutionary center (Argus and McNeill, 1974) and an area of relatively high endemism (e.g., Marie-Victorin, 1938; Morisset, 1971; Argus, 1977; Bouchard et al., 1985). *Fragaria multicipita* appears to be similar to many of the Gulf of St. Lawrence endemics in being a plant of open, disturbed habitats that is rare and characterized by small populations (Marie-Victorin, 1938; Morisset, 1971; Wynne-Edwards, 1939).

MATERIAL EXAMINED: CANADA: **Québec**: Gaspé Ouest Municipality: Cap Chat Township: River Ste. Anne-des-Monts, 14–17 July 1906, *M. L. Fernald & J. F. Collins 230* (HOLOTYPE-GH!, ISOTYPE-GH!); 9 km SSE of Ste.-Anne-des-Monts (hwy 132) beside Rivière Ste.-Anne, 49°04′40″N, 66°29′55″W, 16 July 1992, *P. M. Catling & V. R. Catling 13251* (DAO, MT).

## SIGNIFICANCE

The rediscovery of *F. multicipita* is significant in many respects. It has already resulted in additional information relevant to classification. When portions of 50 plants representing variation in *Fragaria* along the Ste.-Anne rivershore were grown beside each

other in a greenhouse in similar pots and similar soil mix, all retained the distinctive morphological features seen in the field and in some cases these features became even more pronounced. For example, plants referable to *Fragaria multicipita* grew into large runnerless "bushes" with 50–100 ramets, but retained their small size and small nearly stalkless leaflets, and either did not produce runners or produced a few very short runners to 10 cm long. The evidence of localized genetic differentiation, as well as a rather distinct habitat, are consistent with species rank, but the more important point is that there is now living material available for the further assessment of rank and the study of variation.

*Fragaria multicipita* was one of the species used by Fernald (1925) to support his "persistence" or "nunutak" hypothesis, and it was also one of 45 species, potentially supporting the hypothesis, that were screened by Drury (1969). The explanation for, and nature of endemism and unusual patterns of plant variation in the Gulf of St. Lawrence region has still to be thoroughly explored, although recent studies (e.g., Brouillet and Labrecque, 1987; Labrecque and Brouillet, 1990; Houle and Haber, 1990) have contributed much useful information. As a non-halophytic and non-serpentine taxon, *F. multicipita* is especially relevant to the persistence concept and to an understanding of northeastern endemism. Drury (1969) noted that, to advance knowledge in these areas, what was needed most of all were detailed studies of ecology, natural history, and variation of some of the most critical endemic taxa, such as *F. multicipita*.

An understanding of variation in native wild strawberries and the protection of this variation has become more relevant to agriculture over the past several years for two reasons. Firstly, it has become more widely recognized that North American strawberry production has a narrow germplasm base (e.g., Luby et al., 1992). Secondly, the use of native wild strawberry germplasm to increase genetic diversity of cultivated strawberries is increasingly important because of the need to reduce the use of chemicals for disease and pest control, while at the same time increasing production efficiency (e.g., Daubeny, 1990).

Two additional points arise from these considerations. One is that there are in North America important centers of crop-relative diversity where *in situ* protection is desirable, the valley of Rivière Ste.-Anne being an example. Secondly information on patterns of variation within species, that would be useful for purposes of

germplasm protection, are inadequate, even for some of our most familiar native plants such as strawberries.

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# CHROMOSOME NUMBER DETERMINATIONS IN FAM. COMPOSITAE, TRIBE ASTEREAE. V. EASTERN NORTH AMERICAN TAXA

JOHN C. SEMPLE, JIE ZHANG AND CHUNSHENG XIANG

## ABSTRACT

Chromosome numbers are reported for 333 individuals of 109 taxa and two interspecific hybrids from among 11 genera. The vast majority of the reports are for *Aster sensu lato* and *Solidago*. Many counts confirm previous reports for the taxa; approximately one third of the counts are first reports for a taxon, or ploidy level of a taxon, in one or more of the 26 states of the eastern United States and one Canadian province sampled. The cytogeography and cytotaxonomy of the *Aster pilosus*, *Solidago stricta* and *S. uliginosa* complexes are discussed. The following first reports are included: *Aster attenuatus*, $2n = 48$; *A. surculosus*, $2n = 36$; *Solidago latissimifolia*, $2n = 18_{II}$, $2n = 36$, $2n = 27_{II}$, $2n = 54$; *S. patula* var. *strictula*, $2n = 9_{II}$; *S. pulchra*, $2n = 18_{II}$.

Key Words: Compositae, Astereae, chromosome numbers, *Aster*, *Boltonia*, *Conyza*, *Croptilon*, *Chrysopsis*, *Euthamia*, *Gutierrezia*, *Heterotheca*, *Pityopsis*, *Solidago*, *Virgulus*, cytogeography, Canada, United States

## INTRODUCTION

This is the fifth in a continuing series of reports by our laboratory and collaborators on chromosome numbers in the tribe Astereae (Semple, 1985; Semple and Chmielewski, 1987; Semple, Chmielewski and Lane, 1989; Semple, Chmielewski and Xiang, 1992). Determining the distribution patterns of cytotypes requires numerous counts from the range of a taxon. The counts listed in this paper are reported as further contributions to such studies. In this paper, our focus is on taxa native to the eastern and central United States and adjacent Canada.

## MATERIALS AND METHODS

Meiotic counts were made from pollen mother cells dissected from buds fixed in the field in 3:1/EtOH : glacial acetic acid and subsequently stored under refrigeration in 70% EtOH. Mitotic counts were made from root tip cells taken from transplanted wild rootstocks or from seedlings grown from achenes collected in the wild. Root tips were pretreated in 0.01% colchicine or saturated paradichlorobenzene (PDB) for 2–3 hr., fixed in either Modified

Carnoy's Fixative (4:3:1/chloroform : EtOH : glacial acetic acid) or Acetic Alcohol Fixative (3:1/EtOH : glacial acetic acid) and hydrolyzed in 1 N HCl for 30 min. at 60°C before squashing. Both anther sacs containing pollen mother cells and meristematic root tips were squashed in 1% acetic orcein, and counts of chromosomes were made from freshly prepared material. Permanent slides were made in most cases as described by Semple, Brammall and Chmielewski (1981) and remain in Semple's possession.

All counts were made from sporophyte tissue cells and are reported as "$2n =$." Those counts made from late prophase (diplotene and diakinesis) and first metaphase in pollen mother cells undergoing meiosis are followed by "$_{II}$" indicating that pairs of chromosomes were counted, e.g., $2n = 18_{II}$. Many of the taxa studied include polyploids and could be indicated by additional notation, e.g., $2n = 4x = 32$. However, since nearly all, if not all of these cytotypes appear to have undergone diploidization, counts for them are reported without indicating ploidy level.

Vouchers for all counts are deposited in WAT with duplicates distributed to various other herbaria. Identifications were made by Semple. In some cases, the voucher specimens did not agree with published descriptions in one or more minor traits, such as the amount of pubescence or floret color; these cases are indicated by the qualifier "aff." in Table 1.

## RESULTS AND DISCUSSION

Chromosome number determinations from 333 individuals representing 109 taxa and two interspecific hybrids from among 11 genera are reported in Table 1. All location and voucher data are published here for the first time. Populations were sampled in one province in Canada and in 26 states in the United States. In total, 308 of these reports are for asters and goldenrods (*Aster, Virgulus, Solidago* and *Euthamia).* Two-thirds of the counts confirm previous reports for the taxa and most are presented without comment. Included in Table 1 are the following first reports for these taxa: *Aster attenuatus* Lindl., $2n = 48$ (one population) from Texas; *A. surculosus* Michx., $2n = 36$ (one population) from North Carolina; *Solidago latissimifolia* Mill. (one population each), $2n = 18_{II}$ from South Carolina, $2n = 36$ from Massachusetts, $2n = 27_{II}$ from Massachusetts and Rhode Island, $2n = 54$ from Mas-

Table 1. Chromosome number determinations of Astereae from Canada and the United States, arranged alphabetically. *Ah* = Tufail Ahmed; *Ch* = J. G. Chmielewski; *S* = J. C. Semple; *Su* = Bambang Agus Suripto; *Xg* = ChunSheng Xiang. When voucher specimens did not fit a published taxon description in one or more minor traits, the qualifier "aff." is used. State highway numbers are indicated by the standard postal code abbreviation for the state followed by the number. [1] First report for the taxon; [2] first report(s) for the taxon or ploidy level for the particular province or state.

*Aster acuminatus* Michx. $2n = 9_{II}$. **Maine.** York Co.: Lyman, ME-111 0.1 km E of ME-35, *S & Su 9587*.

*A. anomalus* Englemann *in* Torr. & Gray. $2n = 16$. **Arkansas.**[2] Carrol Co.: US-62 W of Berryville, 6.9 km E of AR-23, *S & Su 9950*. **Illinois.** Union Co.: Bald Knob Rd., woods, *S & Su 9877*.

*A. asteroides* (L.) MacMillan (synonym: *A. paternus* Cronq.) $2n = 18$. **North Carolina.** Cherokee Co.: W of Ranger, US-64 7.8 km W of US-129, *S & Jeff Semple 10353* (2 plants).

*A. attenuatus* Lindl. *in* Hook.[1] $2n = 48$. **Texas.** Jasper Co.: E of Woodville, US-190 13.5 km E of US-69, *S & Su 10055*.

*A. avitus* Alex. $2n = 18$. **Georgia.** Dekalb Co.: base of Stone Mt. near access rd to top of mountain, *S & Jeff Semple 10346*.

*A. borealis* (Torr. & Gray) Prov. $2n = 64$. **Ontario.** Kenora Dist.: Peawanuck (S of old Winisk), *Clements s.n.*

*A. chlorolepis* Burgess *in* Small. $2n = 36$. **North Carolina.** Yancey Co.: Mt. Mitchell, midway along rd to park, *S & Su 9684*.

*A. ciliolatus* Lindl. $2n = 48$. **Ontario.** Kenora Dist.: Peawanuck (S of old Winisk), *Clements s.n.*

*A. cordifolius* L. $2n = 16$. **Illinois.** Union Co.: Trail of Tears State For., *S & Su 9882*. **Kentucky.** Allen Co.: US-31 a few mi. S of Petroleum, *S & Ch 9110*. $2n = 32$. **Kentucky.** Adair Co.: NW of Toria, Cumberland Pkwy (MP38.1), *S & Su 9447*. Pulaski Co.: KY-1392 ca. 10 km S of Livingston, bluff of Rockcastle R., *S & Su 9603*. **Oklahoma.**[2] Flore Co.: US-59 just N of Ouachita Nat'l For. boundary, *S & Su 9985*.

*A.* aff. *cordifolius* L. × *A. pilosus* Willd. $2n = 32$. **Ontario.** Waterloo Co.: Wellesley Twp, *S & Ch 9097A*.

*A. depauperatus* (Porter) Fern. $2n = 16$. **North Carolina.** Granville Co.: NE of Butner, along power line right-of-way, *S & Su 9724*.

*A. divaricatus* L. $2n = 9_{II}$. **Pennsylvania.** Perry Co.: PA-74 3 km NW of Ickesberg, *S & Su 9490*. $2n = 18$. **Massachusetts.** Bristol Co.: N of Somerset along Segreganset Estuary, *S 9183*.

*A. drummondii* Lindl. $2n = 16$. **Arkansas.** Carrol Co.: N edge of Berryville, AR-21, corner of Julie St. and Standley Ave. NE, *S & Su 9948*. **Louisiana.**[2] Caddo Parish: LA-2 8.0 km E of Vivian (LA-1), *S & Su 10031*. **Texas.**[2] Lamar Co.: Brackeen Cemetery Rd. off TX-19, *S & Su 10003*. Newton Co.: NE of Burkeville, TX-63 2.5 km W of Sabine R., *S & Su 10049*. $2n = 32$. **Illinois.** Kakankee Co.: NW of Bradley, Kakankee State Park, along Rock R., *S & Su 9867*. St. Clair Co.; Fairview Heights, community park, *S & Su 9406*. **Mississippi.**[2] Adams Co.: SE of Natches, Fire Tower Rd. just E of US-91, *S*

Table 1. Continued.

*& Su 10087*. **Texas.**[2] Anderson Co.: US-84 17.6 km E of Palestine city limits (Loope Rd-56), *S & Su 10016*.

*A. dumosus* L. $2n = 8_{II}$. **North Carolina.** Bertie Co.: SE of Bertie, NC-308 9.8 km SE of US-17, *S & Su 9742*. Yadkin Co.: WSW of Yadkinville, US-421 ca. 1 km E of US-21, *S & Su 9708* & *S & Su 9709*. $2n = 16$. **Kentucky.** Pulaski Co.: KY-1392 ca. 10 km S of Livingston, bluff of Rockcastle R., *S & Su 9604*. **Louisiana.** Concordia Parish, W of Ferriday, US-84 6 km W of LA-15, vicinity of picnic area, *S & Su 10069*. **Massachusetts.** Essex Co.: N of Newbury, by airport, ca. 1.5 km W of Plum Is. R., *S & Su 9574*. **Mississippi.** Amite Co.: NE of Liberty, Holmes Rd. 6.7 km SE of MS-570, *S & Su 10102*. $2n = 32$. **Arkansas.** Franklin Co.: N of Ozark, AR-23 just S of I-40, *S & Su 9966*. Sebastian Co.: AR-28 4.6 km E of Cauthron, 14 km W of US-71, *S & Su 9980*. **Louisiana.** Vernon Parish: US-171 3.4 km N of Anacoco (LA-111), *S & Su 10041*. **Oklahoma.**[2] McCurtain Co.; US-70 3.5 km E of Valiant, W of Millerton, *S & Su 9995*. **South Carolina.** Clarendon Co.: US-521 1.1 km SE of Wilson, *S & Su 9784*. **Texas.**[2] Newton Co.: NE of Burkeville, TX-63 2.5 km W of Sabine R., *S & Su 10048*.

*A. gracilis* Nutt. $2n = 9_{II}$. **New Jersey.** Burlington Co.: N of Chatsworth, Co. Rd.-563 0.9 km S of NJ-72, *S 10365*; S of Chatworth, local road to cranberry bog, *S 10369*. Ocean Co.: W of Barnegat, Co. Rd.-554 2.4 km W of Garden State Parkway, *S & Su 9516*.

*A. hemisphaericus* Alex. in Small. $2n = 18$. **Mississippi.** Franklin Co.: US-98 just E of MS-570, *S & Su 10101*.

*A. laevis* L. var. *laevis* × *A. lanceolatus* Willd. ssp. *lanceolatus* var. *lanceolatus*. $2n = 48$. **Ontario.** Kent Co.: Hwy-3, Port Crewe, *S & Ch 9138*.

*A. lanceolatus* Willd. ssp. *lanceolatus* var. *hirsuticaulis* Semple & Chmielewski. $2n = 32$. **Wisconsin.** Douglas Co.: US-2 E of Maple, *S 9047-2*.

*A. lanceolatus* Willd. ssp. *lanceolatus* var. *interior* (Wieg.) Semple & Chmielewski. $2n = 48$. **Arkansas.**[2] Logan Co.: SW of Booneville, AR-23 2.2 km E of Carolan Cemetery, *S & Su 9976*. **Illinois.** White Co.: S of Norris City, junction of IL-1 and US-45, *S & Su 9423*. $2n = 64$. **Kentucky.**[2] Webster Co.; KY-109 1.7 km W of Clay, *S & Su 9428*.

*A. lanceolatus* Willd. ssp. *lanceolatus* var. *latifolius* Semple & Chmielewski. $2n = 64$. **Illinois.** Franklin Co.: IL-149 1.7 km W of Zeigler (IL-148). *S & Su 9875*. **Indiana.** Putnam Co.: SE of Cloverdale, IN-42 4.1 km W of US-231, *S & Su 9401*. **Kentucky.**[2] Robertson Co.: KY-617 0.5 km W of Piqua, banks of Bluelick R., *S & Su 9593*. Webster Co.; KY-109 1.7 km W of Clay, *S & Su 9427*.

*A. lanceolatus* Willd. ssp. *lanceolatus* aff. var. *latifolius* Semple & Chmielewski. $2n = 64$. **Alabama.**[2] Montgomery Co.: SE of Montgomery, US-321 0.7 km SE of US-82 *S & Su 10155*. The rays are blue and the phyllaries are less graduated than typical for the variety).

*A. lateriflorus* (L.) Britt. $2n = 16$. **Missouri.** Carter Co.: US-60 1.8 km E of Van Buren *S & Su 9907*. **Oklahoma.** Flore Co.: US-59 just N of Ouachita Nat'l For. boundary, river bank, *S & Su 9984*. $2n = 32$. **Alabama.** Dale Co.: E of Clayhatchee, US-84 at Little Choctawhatchee R., *S & Su 10152*. **Illinois.**

Table 1. Continued.

Hamilton Co.: IL-142 1 km SE of Dahlgreen, *S & Su 9419*. **Kentucky.** Estill Co.: KY-52 E of Ravenna, *S & Su 9457*. Hopkins Co.: KY-109 1 km N of Charleston, *S & Su 9430*. Pulaski Co.: KY-1392 ca. 10 km S of Livingston, bluff slope of Rockcastle R., *S & Su 9601*, **Missouri.** Douglas Co.: MO-14 at Twin Bridges (MO-181), along N. Fork of White R., *S & Su 9927*. **Tennessee.** Montgomery Co.: US-79 0.5 km S of Kentucky state line, *S & Su 9435*. **Texas.** Rusk Co.: US-84 6.4 km E of Reklaw, *S & Su 10023*.

*A. linariifolius* L. $2n = 9_{II}$. **Louisiana.** Rapides Parish: N of Forest Hill, LA-112 2.1 km W of US-165, *S & Su 10090*. **Maine.** Sagadahoc Co.: NW of Popham Beach, junction of ME-209 and ME-216, *S 10378*. **Massachusetts.** Barnstable Co.: Harwich, Queen Anne Rd 2 km NE of Old Chatham Rd., *S & Su 9559*. **New Jersey.**[2] Atlantic Co.: US-40 5.6 km W of Mays Landing (NJ-42), *S & Su 9504*. **South Carolina.** Berkeley Co.: SC-45 ca. 5 km E of St. Stephen, Francis Marion Nat'l For., *S & Su 9794*.

*A. nemoralis* Ait. $2n = 9_{II}$. **Maine.** Sagadahoc Co.: W Popham Beach, ME-209 2 km E of ME-216, *S 10380*.

*A. novi-belgii* L. $2n = 48$. **Maine.** York Co.: Wells, vicinity of Municipal Offices, *S & Su 9581*.

*A. ontarionis* Wieg. $2n = 32$. **Tennessee.** Marshall Co.: Henry Horton State Park, *S & Ch 9117*. Montgomery Co.: NE of Clarkville, US-79 0.5 km S of Kentucky state line, *S & Su 9436*.

*A. oolentangiensis* Riddell. $2n = 32$. **Illinois.** St. Clair Co.; Fairview Heights, community park, *S & Su 9407*. **Missouri.** Oregon Co.: MO-19 16.6 km S of US-60, N of Greer, *S & Su 9911*. Wayne Co.: Co. Rd.-F 0.1 km E of US-67, 7.8 km S of Greenville, *S & Su 9894*. **Oklahoma.** McCurtain Co.: US-259 20.9 km N of Broken Bow, *S & Su 9990*.

*A.* aff. *parviceps* (Burgess) Mackenzie & Bush. [See text for discussion of these collections.] $2n = 32$. **Missouri.** Washington Co.: MO-8 6.6 km W of Potosi, *S, Su & Ah 9393*.

*A.* aff. *pilosus* Willd. var. *pringlei* (A. Gray) Blake. [See text for discussion of these collections.] $2n = 48$. **Missouri.**[2] Oregon Co.: N of Greer, MO-19 16.6 km S of US-60, Mark Twain Nat'l For., vicinity of For. Rd.-3174, *S & Su 9912*. Taney Co.: MO-76 12.6 km W of county line, cedar glade, *S & Su 9938*. Wayne Co.: Co. Rd.-F 0.1 km E of US-67, 7.8 km S of Greenville, *S & Su 9892*.

*A. pilosus* Willd. var. *pilosus*. $2n = 32$. **Ontario.** Essex Co.: Colchester N. Twp. Essex-12 5 km SW of Gesto, SW of Canard R., *S & Ch 9145*. **Arkansas.** Madison Co.: S of Eureka Spring, AR-23 1.8 km S of county line, *S & Su 9955*. **Illinois.** 7.5 km E of McLeansboro at Co. Rd.-1400E, *S & Su 9422*. **Kentucky.** Nicholas Co.: Bluelick Battlefield State Park, *S & Su 9596*. Warren Co.: US-68 at Logan Co. line, vicinity of quarry, *S & Su 9441*. **North Carolina.** Avery Co.: E of Linville, top of Grandfather Mt., edge of parking lot, *S & Su 9672*. $2n = 48$. **Illinois.** Hamilton Co.: IL-142 1.0 km SE of Dahlgreen, *S & Su 9417*. **Oklahoma.**[2] McCurtain Co.: W of Millerton, US-70 3.5 km E of Valiant, *S & Su 9994*.

*A. pilosus* Willd. aff. var. *pringlei* (A. Gray) Blake. $2n = 48$. **Massachusetts.** Barnstable Co.: East Brewster, along Bike Trail W of Nickerson State Park,

Table 1. Continued.

near MA-6A, *S & Su 9551*. (The plant is more hairy than typical but not as hairy as var. *pilosus*.)

*A. praealtus* Poir. var. *praealtus*. $2n = 32$. **Mississippi.** Amite Co.: NE of Liberty, Holms Rd., *S & Su 10105*. **Missouri.** Greer Co.: SE of Walnut Grove, MO-123 at Farm Rd-56, *S & Su 9946*. **Oklahoma.** McCurtain Co.: US-70 E edge of Idabel, *S & Su 9993*. $2n = 48$. **Texas.** Lamar Co.: US-271 S of Powderly, N of Paris, N of Loop-Rd.-287, *S & Su 9999*.

*A. prenanthoides* Muhl. $2n = 32$. **Kentucky.** Laurel Co.: along Rockcastle R. above mouth of Blair Branch Creek, *S & Su 9854*. Menifee Co.: Boone Nat'l For., KY-715 along river, *S & Su 9465*. **Tennessee.**[2] Unicoi Co.: E of Unicoi, TN-107 5.2 km E of TN-173, *S & Su 9632*.

*A. priceae* Britt. $2n = 64$. **Kentucky.**[2] Logan Co.: Russellville, US-68 just N of US-431, glade, *S & Su 9438*. Warren Co.: US-68 at Logan County line, by quarry, *S & Su 9440-1*.

*A. puniceus* L. $2n = 16$. **Georgia.**[2] Rabun Co.: US-76 ca. 3 km W of Clayton, *S & Su 9830*. **Minnesota.** Pine Co.: MN-18 E of N end of Big Pine Lake, near county line, *S 9069*. **North Carolina.** Avery Co.: W of Linville, Grandfather Mt., near Black Rock Hiking Trail, *S & Su 9673*. **Tennessee.**[2] Unicoi Co.: E of Unicoi, TN-107 0.3 km W of NC state line, *S & Su 9642*.

*A. racemosus* Ell. [Specimens treated in most floras under the misapplied name *A. vimineus* Lam.] $2n = 8_{II}$. **North Carolina.** Chowan Co.: NC-37 just N of Albermarle Sound Causeway, *S & Su 9747*. $2n = 16$. **Alabama.**[2] Montgomery Co.: SE of Montgomery, US-231 0.7 km SE of US-82, *S & Su 10156*. Tuscaloosa Co.: US-82 2.4 km W of US-43, W of Northport, NW of Tuscaloosa, *S & Su 10162*. **Arkansas.** Washington Co.: US-71, rest area N of Brentwood, *S & Su 9959*. **Kentucky.**[2] Webster Co.: KY-109 1.7 km W of Clay, *S & Su 9429*. **Louisiana.**[2] East Feliciana Parish: S of Felps, LA-67 2.5 km S of LA-422, *S & Su 10107*. Red River Parish: N of Edgefield, LA-7 11.2 km S of county line, *S & Su 10036*. **Mississippi.** Franklin Co.: NW of Roxie, US-84 1.5 km W of MS-33, *S & Su 10098*. Monroe Co.: S of Becker, MS-25 0.9 km N of MS-8, *S & Su 10167*. **Missouri.**[2] Wayne Co.: Co. Rd.-F 0.1 km E of US-67, 7.8 km S of Greenville, *S & Su 9895*. **Texas.** Anderson Co.: US-84 17.6 km E of Palestine city limit (Loop Rd-56), *S & Su 10017*. Grimes Co.: TX-105 2.6 km W of Plantersville, *S & Su 10064*. San Jacinto Co.: TX-150 3.6 km E of Shepherd, *S & Su 10062*. $2n = 32$. **North Carolina.** Durham Co.: N of Durham, by Eno R., Penny's Head Nature Res., *S & Su 9718*.

*A. reticulatus* Pursh. $2n = 18$. **Florida.** Leon Co.: S of Bloxham, Appalachicola N.F., For. Rd.-320 just E of Co. Rd.-375 (T1S, R4W, Sec. 32), *S & Jeff Semple 10342*.

*A. retroflexus* Lindl. *in* DC. $2n = 48$. **North Carolina.** Mitchell Co.: NC-226 0.5 km E of Tennessee state line, *S & Su 9648*. Watauga Co.: W of Blowing Rock, *S & Su 9681*. **Tennessee.** Unicoi Co.: TN-107 17 km E of Unicoi, *S & Su 9643*.

*A. sericocarpoides* (Small) K. Schum. $2n = 18$. **South Carolina.**[2] Chesterfield Co.: US-1 just NE of entrance to Cheraw Fish Hatchery, *S & Su 9780*.

*A. shortii* Lindl. *in* Hook. $2n = 16$. **Illinois.** Kakankee Co.: NW of Bradley, Kakankee R. State Park, woods by Rock R., *S & Su 9868*. **Kentucky.** Adair

Table 1. Continued.

Co.: NW of Toria, Cumberland Parkway (MP38.1) W of KY-80, *S & Su 9449*. $2n = 32$. **Indiana.** Putnam Co.: SE of Cloverdale, IN-42 4.1 km W of US-231, *S & Su 9402*. **Kentucky.** Christian Co.: KY-109 SE of Dawson Spring, Pennyrite For. State Park, *S & Su 9433*. Warren Co.: S of Alvaton, US-231 2.8 km S of Co. Rd.-961, *S & Ch 9105*.

*A. solidagineus* Michx. $2n = 18$. **North Carolina.** Cherokee Co.: US-64 7.8 km W of Ranger (US-129), *S & Jeff Semple 10352* (3 plants).

*A. spectabilis* Ait. $2n = 36_{II}$. **Massachusetts.** Plymouth Co.: W of Cedarville, Long Pond Rd. 0.3 km N of Carters Bridge Rd., N of Great Herring Lake, *S & Su 9567*.

*A. subulatus* L. var. *subulatus*. $2n = 5_{II}$. **New Jersey.** Ocean Co.: Tuckerton, cedar marsh E of town center, *S & Su 9525*.

*A. surculosus* Michx.[1] $2n = 36$. **North Carolina.**[2] Cherokee Co.: SE of Ranger, US-19 2.35 km S of US-64, W of Ranger, *S & Jeff Semple 10350*.

*A. texanus* Burgess *in* Small. $2n = 32$. **Texas.** Grimes Co.: TX-105 2.6 km W of Plantersville, *S & Su 10065*.

*A.* aff. *texanus* Burgess *in* Small. $2n = 32$. **Texas.** Jasper Co.: US-190 at Farm Rd-256, W of TX-63, *S & Su 10054*.

*A. tortifolius* Michx. $2n = 9_{II}$. **South Carolina.** Jasper Co.: SC-652 14.9 km SE of Pineland, *S & Su 9804*.

*A. turbinellus* Lindl. $2n =$ ca. 96. **Missouri.** Washington Co.: MO-8 6.6 km W of Potosi. *S, Su & Ah 9392*.

*A. umbellatus* Mill. var. *umbellatus*. $2n = 9_{II}$. **Connecticut.**[2] New London Co.: Waterford, Waterford Conservation Area, Nevins Brook, *S 9191*. **Massachusetts.**[2] Essex Co.: N of Newbury, ca. 1.5 km W of Plum Is. R., opposite airport, *S & Su 9573*.

*A. undulatus* L. $2n = 9_{II}$. **South Carolina.** Berkeley Co.: SC-45 ca. 5 km E of St. Stephen, Francis Marion Nat'l For., *S & Su 9793*. $2n = 32$. **Kentucky.** Adair Co.: NW of Toria, Cumberland Parkway (MP38.1) W of KY-80, *S & Su 9448*. **North Carolina.** Watauga Co.: US-421 at Wilkes Co. line, *S & Su 9701*.

*A. urophyllus* Lindl. *in* DC. $2n = 16$. **Arkansas.**[2] Carrol Co.: W of Berryville, US-62 6.9 km E of AR-23, *S & Su 9949*. **Minnesota.** Hennepin Co., Eden Prairie, Spring Rd. just W of county airport, *S et al. 8851*. **Missouri.** Carter Co.: between Hunter and Van Buren, gravel extension of MO-T 7.8 km SW of US-60, *S & Su 9903*. Hickory Co.: E of Wheatland, US-54 0.9 km E of Hicomo Picnic Area, *S & Su 9943*. Wayne Co.: E of Williamsville, MO-49 4.4 km E of Co. Rd-A, *S & Su 9901*.

*Boltonia asteroides* (L.) L'Her. var. *recognita* (Fern. & Griscom) Cronq. $2n = 18$. **Illinois.** Hamilton Co.: IL-142 1 km SE of Dahlgreen, *S & Su 9415*; IL-142 8.5 km SE of Dahlgreen, *S & Su 9420*.

*Conyza canadensis* (L.) Cronq. var. *canadensis*. $2n = 18$. **Ontario.** Waterloo Regional Mun.: Waterloo, University of Waterloo, north campus greenhouse, weed in pot, *S 1038x*.

*Croptilon divaricatum* (nutt.) Raf. $2n = 4_{II}$. **North Carolina.** Pitt Co.: W of Bethel, US-64 0.2 km E of Edgecombe Co. line, *S & Su 9736*.

Table 1. Continued.

*Chrysopsis gossypina* (Michx.) Ell. ssp. *gossypina* f. *gossypina*. $2n = 9_{II}$. **North Carolina.** Pender Co.: Hampstead, NC-210 0.9 km W of US-17, *S & Su 9758*.

*C. gossypina* (Michx.) Ell. ssp. *gossypina* f. *trichophylla* (Nutt.) Semple. $2n = 9_{II}$. **North Carolina.**[2] Bladden Co.: NC-53 20 km SE of US-701, *S & Su 9773*.

*C. mariana* (L.) Ell. $2n = 12_{II}$. **New Jersey.** Atlantic Co.: US-40 5.6 km W of Mays Landing (Hwy-52), *S & Su 9503*. **Louisiana.** Beauregard Parish: LA-12 11.8 km W of Ragley (US-171), 1.4 km W of Gordon Fire Tower, *S & Su 10089*. **North Carolina.** Bertie Co.: SE of Bertie, NC-308 9.8 km SE of US-17, *S & Su 9742*. **South Carolina.** Colleton Co.: NW of Jacksonboro, NC-64 ca. 2.5 km NW of US-17, *S & Su 9799*.

*Euthamia leptocephala* (Torr. & Gray) Greene. $2n = 18$. **Texas.** Navarro Co.: W of Eureka, US-287 3.3 km W of Farm Rd.-637, *S & Su 10010*. Newton Co.: TX-63 2.5 km W of Sabine R., NE of Burkeville, *S & Su 10050*. Polk Co.: E of Livingstone, US-190 1.8 km E of Soda, 16.4 km E of TX-146, *S & Su 10061*.

*E. tenuifolia* (Pursh) Nutt. $2n = 18$. **North Carolina.** Franklin Co.: NC-56 4.2 km W of county line, *S & Su 9731*. **South Carolina.**[2] Hampton Co.: SC-68 11 km NW of Yemasee, *S & Su 9802*.

*Gutierrezia texana* (DC.) Torr. & Gray var. *texana*. $2n = 4_{II}$. **Texas.** Dallas Co.: N of Cedar Hill, Cedar Hill Rd. opposite lot No. 1110, RR right-of-way, *S & Su 10008*.

*Heterotheca camporum* (Greene) Shinners var. *glandulissimum* Semple. $2n = 36$. **Alabama.**[2] Limestone Co.: Littleville, US-43 at N city limits, *S & Su 10178*. **Arkansas.** Carrol Co.: NE of Oak Grove, AR-21 just S of Blue Eye, *S & Su 9947*. **Missouri.**[2] Christian Co.: Ozark, MO-14 just E of US-65, *S & Su 9939*.

*H. subaxillaris* Lam. $2n = 9_{II}$. **New Jersey.**[2] Salem Co.: W of Malaga, NJ-55, *S & Su 9498*.

*Pityopsis falcata* (Pursh) Nutt. $2n = 9_{II}$. **Massachusetts.** Barnstable Co.: Cape Cod, East Brewster, by Bike Trail W of Nickerson State Park, near MA-6A, *S & Su 9762*.

*P. graminifolia* (Michx.) Nutt. var. *latifolia* (Fern.) Semple & Bowers. $2n = 18_{II}$. **North Carolina.** Chowan Co.: NC-37 just N of Albermarle Sound Causeway, SE of Edenton, *S & Su 9746*. Pender Co.: Hampstead, NC-210 ca. 4.1 km W of US-17, *S & Su 9762*.

*P. graminifolia* (Michx.) Nutt. var. *tenuifolia* (Torr.) Semple & Bowers. $2n = 9_{II}$. **Louisiana.**[2] Beauregard Parish: LA-12 SE of DeQuincy, *S & Su 10083*. East Feliciana Parish: E of Woodland, LA-432 1.5 km E of LA-67, *S & Su 10113*.

*P. oligantha* (Chapm.) Small. $2n = 36$. **Florida.** Franklin Co.: W of St. Teresa, US-319 2.7 km S of Ochlockonee R., *S & Jeff Semple 10340*.

*Solidago altissima* L. var. *altissima*. $2n = 36$. **Texas.**[2] Grimes Co.: TX-105 1.5 km E of TX-Farm Rd-362, *S & Su 10069*. Harris Co.: N of Bayton, I-10 rest

Table 1. Continued.

area, *S & Su 10076*. Lamar Co.: S of Powderly, US-271 N of Loop Rd-286, *S & Su 10002*. $2n = 54$. **Illinois.** Hamilton Co.: IL-142 1 km SE of Dahlgreen, *S & Su 9418*. **Kentucky.** Christian Co.: KY-109 SE of Dawson Spring, N end of Pennyrite Forest State Park, *S & Su 9434-1*. Harrison Co.: US-62 2 km SW of Clayville, *S & Su 9592*. **Louisiana.** Vernon Parish: N of Anacoco, US-171 3.4 km N of LA-111, *S & Su 10046*. **Missouri.** Washington Co.: NE of Potosi. MO-21 just N of MO-8, *S, Su & Ah 9395*. **North Carolina.** Jones Co.: Chadwick, US-17 ca. 5 km NE of Maysville, *S & Su 9753*. Pitt Co.: W of Bethel, US-64 0.2 km W of county line, *S & Su 9737*. **South Carolina.**[2] Colleton Co.: NW of Jacksonboro, NC-64 2.5 km from US-17, *S. & Su 9800*. **Tennessee.**[2] Montgomery Co.: US-79 0.5 km S of Kentucky state line, ca. 12 km NE of Clarkville, *S & Su 9437*.

*S. arguta* Ait. ssp. *arguta*. $2n = 9_{II}$. **Pennsylvania.** Juniata Co.: 5 km NW of Ickesberg, ridge top, *S & Su 9485*.

*S. arguta* Ait. ssp. *caroliniana* (A. Gray) G. Morton. $2n = 9_{II}$. **South Carolina.** Berkeley Co.: SC-45 ca. 5 km E of St. Stephen, Francis Marion Nat'l For., *S & Su 9792*. $2n = 18$. **Mississippi.**[2] Amite Co.: NE of Liberty, Holmes Rd. 6.7 km SE of MS-570, *S & Su 10104*. **Missouri.**[2] Taney Co.: MO-76 11.8 km W of county line, *S & Su 9935*. $2n = 36$. **Kentucky.** Adair Co.: NW of Toria, Cumberland Parkway (MP38.1), *S & Su 9444*. Laurel Co.: Daniel Boone St. For. junction of For. Rd.-119 and For. Rd-56, *S & Su 9613*.

*S. bicolor* L. $2n = 9_{II}$. **Maine.** Sagadahoc Co.: S of Bath, Meadowbrook Rd., woods above The Basin tidal basin, *S 10377*. **Pennsylvania.**[2] Perry Co.: PA-74 3 km NW of Ickesberg, *S & Su 9487*.

*S. caesia* L. $2n = 18$. **Indiana.** Putnam Co.: SE of Cloverdale, IN-42 4.1 km W of US-231, *S & Su 9403*. **Kentucky.** Powell Co.: Boone Nat'l For. Tunnel Ridge Rd., *S & Su 9462*. **North Carolina.**[2] Durham Co.: N of Durham, Penny's Bend Nature Reserve, Eno R., *S & Su 9720*.

*S. canadensis* L. var. *canadensis*. $2n = 9_{II}$. **Massachusetts.** Plymouth Co.: E of Raynham, MA-104 just S of Lake Nippennicket, *S 9181*.

*S. delicatula* Small. $2n = 18$. **Texas.** Anderson Co.: Co. Rd.-494 0.5 km W of US-287, 3.5 km W of Cayuga, *S & Su 10014*.

*S. erecta* Pursh. $2n = 9_{II}$. **New Jersey.** Atlantic Co.: US-40 5.6 km W of Mays Landing, *S & Su 9501*. **North Carolina.** Franklin Co.: NC-56 4.2 km W of county line, *S & Su 9735*. $2n = 18$. **Kentucky.**[2] Estill Co.: E of Ravenna, KY-52 by Ravenna-Pryse Rd., *S & Su 9454*. Pulaski Co.: KY-1392 ca. 10 km S of Livingston, bluff of Rockcastle R., *S & Su 9605*. **Mississippi.**[2] Itawamba Co.: MS-23 10.1 km N of Tremont, *S & Su 10175*.

*S. fistulosa* Mill. $2n = 9_{II}$. **North Carolina.** Martin Co.: US-64 just W of Parmele, *S & Su 9739*. $2n = 18$. **Alabama.**[2] Mobile Co.: N of Theodore, Co. Rd-59 ca. 2 km S of I-10, *S & Su 10128*. **Mississippi.**[2] Harrison Co.: N of D'Iberville, MS-67 N of I-10, *S & Su 10125*. **New Jersey.** Atlantic Co.: swampy woods by NJ-50 just S of US-40, *S & Su 9506*. **North Carolina.** Jones Co.: Chadwick, US-17 ca. 5 km NE of Maysville, *S & Su 9751*. **South Carolina.** Clarendon Co.: US-521 1.1 km SE of Wilson, *S & Su 9785*.

*S. flexicaulis* L. $2n = 36$. **Kentucky.** Estill Co.: KY-52 E of Ravenna on Ravenna-Pryse Rd., *S & Su 9453*. Menifee Co.: Boone, N.F., KY-715, river bank,

Table 1. Continued.

*S & Su 9464.* Pulaski Co.: KY-1392 ca. 10 km S of Livingston, bluff of Rockcastle R., *S & Su 9606.*

*S.* aff. *flexicaulis* L. $2n = 90$.[1] **Kentucky.** Leslie Co.: S of Stinnett, US-421 just S of where highway crosses river, *S & Su 9619.* [The plant was tall for the species and the heads were very large.]

*S. gigantea* Ait. $2n = 18$. **Kentucky.**[2] Leslie Co.: US-421 S of Stinnett, *S & Su 9620.* **Mississippi.** Lowndes Co.: Columbus, N end of tow, US-45 S of Chapman Rd., *S & Su 10165.* **North Carolina.** Franklin Co.: NC-56 4.2 km W of Nash County line, *S & Su 9732.* Washington Co.: E of Skinnerville, US-64 just W of NC-32, *S & Su 9748.* **South Carolina.**[2] McCormick Co.: 4 km N of McCormick, along side rd off SC-28, *S & Su 9819.* $2n = 36$. **Illinois.** Kakankee Co.: NW of Bradley, Kakankee R. State Park, *S & Su 9871.* White Co.: S of Norris City, junction of IL-1 and US-45, *S & Su 9424.* **Missouri.**[2] Douglas Co.: MO-14 at Twin Bridges (MO-181), woods by N. Fork White R., *S & Su 9928.* Hickory Co.: E of Wheatland, US-54 ca. 0.9 km E of Hicomo Picnic Area, *S & Su 9945.* $2n = 54$. **Nebraska.**[2] Hooker Co.: N of Mullen, NE-97 at Middle Loup R., *S, Su & Ah 9200.*

*S. glomerata* Michx. $2n = 108$. **North Carolina.** Avery Co.: W of Linville, Grandfather Mt., cliff face at top of mt. SW of swing bridge parking lot, *S & Su 9670*; ca. 5000 ft. el., *S & Su 9676.* Mitchell Co.: top of Roan Mt., Roan High Bluff, 6250 ft. el., *S & Su 9661.* Yancey Co.: Mt. Mitchell, near top, ca. 6000 ft. el., *S & Su 9685*; midway along rd. to park, mid el., *S & Su 9683.*

*S. gracillima* Torr. & Gray. $2n = 9_{II}$. **South Carolina.**[2] Barnwell Co.: NW of Barnwell, US-278 just N of Salkehatchie R., *S & Su 9814.*

*S. hispida* Muhl. $2n = 18$. **Ontario.** Kenora Dist.: Peawanuck, *Clements s.n.*

*S. juncea* Ait. $2n = 18$. **Illinois.**[2] Jefferson Co.: S of Mt. Vernon, I-64, *S & Su 9414.* Effingham Co.: Shelbyville, 2.5 km S of Sigel, *S & Su 9874.* **Massachusetts.** Bristol Co.: vicinity of Horseneck Beach Park, *S 9187.* Plymouth Co.: E of Raynham, MA-104 just S of Lake Nippenicket, *S 9182.*

*S. houghtonii* Torr. & Gray. $2n = 9_{II}$. **Ontario.** Bruce Co.: Bruce Peninsula, N of Dyer Bay, alvar below Cabot Head, *S 10363.*

*S. latissimifolia* Mill. $2n =$ ca. $18_{II}$.[1] **South Carolina.** Chesterfield Co.: US-1 just SW of US-52, *S & Su 9778.* $2n = 36$.[1] **Massachusetts.** Plymouth Co.: Center Hill Rd. 2.6 km N of MA-3A, *S & Brouillet 3553.* $2n = 27_{II}$.[1] **Rhode Island.** Washington Co.: E of Charleston, W of Matunuck, near W end of Cards Pond Rd., *S & Su 9544.* $2n = 54$.[1] **Massachusetts.** Plymouth Co.: W of Manomet, Beaver Dam Rd. 0.9 km S of MA-3A, *S & Su 9568.*

*S. leavenworthii* Torr. & Gray. $2n = 36$. **South Carolina.** Allendale Co.: Yemome, US-278 S of Barnwell, *S & Su 9807.*

*S. lepida* DC. $2n = 18$. **Ontario.**[2] Kenora Dist.: Peawanuck (S of old Winisk), *Clements s.n.-1, Clements s.n.-2.*

*S. ludoviciana* (A. Gray) Small. $2n = 18$. **Texas.**[2] Fort Bend Co.: TX-36 5 km S of county line, just N of Farm Rd.-1489, *S & Su 10074.* $2n = 36$. **Texas.** Grimes Co.: TX-105 2.6 km W of Plantersville, *S & Su 10066.* Polk Co.: US-190 E of Livingstone, 1.8 km E of Soda (16.4 km E of TX-146), *S & Su 10058.*

*S. missouriensis* Nutt. $2n = 9_{II}$. **South Dakota.** Minnehaha Co.: NW of Hum-

Table 1. Continued.

boldt, SD-38 3.5 km W of SD-19, *S & Xg 10182*. $2n = 18$. **Nebraska.** Lincoln Co.: NE-97 24.2 km SE of Tyron, *S, Su & Ah 9195*.

*S. mollis* Bartl. var. *mollis*. $2n = 18_{II}$. **South Dakota.** Minnehaha Co.: NW of Humboldt, SD-38 3.5 km W of SD-19, *S & Xg 10181*.

*S. nemoralis* Ait. ssp. *decemflora* (DC.) Brammall in Semple. $2n = 18_{II}$. **South Dakota.** Minnehaha Co.: NW of Humboldt, SD-38 3.5 km W of SD-19, *S & Xg 10181*.

*S. nemoralis* Ait. ssp. *nemoralis*. $2n = 9_{II}$. **North Carolina.** Chowan Co.: NC-37 just N of Albermarle Sound Causeway, SE of Edenton, *S & Su 9745*. Jones Co.: US-17 ca. 5 km NE of Maysville, *S & Su 9750*. **South Carolina.** Berkeley Co.: SC-45 ca. 5 km E of St. Stephen, *S & Su 9790*. $2n = 18$. **North Carolina.** Guilford Co.: E of Greensborough, service rd. W of Rock Creek Dairy Rd. exit off I-40, *S & Su 9713*. $2n = 36$. **Kentucky.** Pulaski Co.: KY-1392 ca. 10 km S of Livingston, bluff of Rockcastle R., *S & Su 9609*.

*S. nitida* Torr. & Gray. $2n = 18$. **Louisiana.** Vernon Parish: N of Anacoco, US-171 3.4 km N of LA-111, *S & Su 10045*.

*S. odora* Ait. var. *odora*. $2n = 9_{II}$. **Louisiana.**[2] Webster Parish. LA-159 8.4 km S of Leton (LA-2), *S & Su 10034*. **Massachusetts.** Bristol Co.: vicinity of Horseneck Beach Park, *S 9186*. **New Jersey.**[2] Salem Co.: W of Malaga, NJ-55, *S & Su 9499*. **South Carolina.**[2] Colleton Co.: NW of Jacksonboro, NC-64 ca. 2.5 km from US-17, *S & Su 9798*. $2n = 18$. **Kentucky.**[2] Powell Co.: Boone Nat'l For., end of Tunnel Ridge Rd., *S & Su 9460*. **Texas.**[2] Newton Co.: NE of Burkeville, TX-63 2.5 km W of Sabine R., *S & Su 10050*.

*S. patula* Muhl. ex Willd. var. *patula*. $2n = 9_{II}$. **New York.** Steuben Co.: W of Bath, county rd., *S & Su 9473*. $2n = 18$. **North Carolina.** Mitchell Co.: top of Roan Mt., *S & Su 9655*. Yancey Co.: Mt. Mitchell, midway along rd. to park, *S & Su 9686*.

*S. patula* Muhl. ex Willd. var. *strictula* Torr. & Gray.[1] $2n = 9_{II}$. **Mississippi.** Harrison Co.: US-46 12 km N of Lyman, *S & Su 10123*.

*S. puberula* Nutt. var. *puberula*. $2n = 9_{II}$. **Maine.** Sagadahoc Co.: S of Bath, Meadowbrook Rd., woods above The Basin tidal basin, *S 10376*. York Co.: NW of Kennebunk, ME-35 1.1 km S of ME-111, Lyman, *S & Su 9586*.

*S. puberula* Nutt. var. *pulverulenta* (Nutt.) Chapm. $2n = 9_{II}$. **North Carolina.**[2] Bladden Co.: 0.5 km SW of Carvers, *S & Su 9771*. **South Carolina.**[2] Barnwell Co.: NW of Barnwell, US-278 just N of Salkehatchie R., *S & Su 9813*.

*S. pulchra* Small.[1] $2n = 18_{II}$. **North Carolina.** Brunswick Co.: NC-133 S of Orton Plantation, *S & Su 9765*. Onslow Co.: US-17 1.7 km N of Dixon (NC-210), *S & Su 9755*. Pender Co.: Hampstead, NC-210 ca. 4.1 km W of US-17, *S & Su 9760*.

*S. radula* Nutt. $2n = 18$. **Louisiana.** Natchitoches Parish: E of Ajax, LA-174 1.5 km SE of co. line, *S & Su 10038*. **Missouri.**[2] Washington Co.: MO-8 6.6 km W of Potosi, *S, Su & Ah 9388*.

*S. rigida* L. var. *glabrata* (Braun) Heard & Semple. $2n = 9_{II}$. **Texas.** Dallas Co.: N of Cedar Hill, Cedar Hill Rd., opposite lot 1110, RR right-of-way, *S & Su 10007*.

*S. rigida* L. var. *humilis* (Porter) Heard & Semple. $2n = 18$. **Illinois.** St. Clair

Table 1. Continued.

Co.: Fairview Heights, Community Park, *S & Su 9413*. **Nebraska.** Hooker Co.: N of Mullen, NE-97 by Middle Loup R., *S, Su & Ah 9198*.

*S. rupestris* Raf. $2n = 36$. **Kentucky.**[2] Robertson Co.: KY-617 0.5 km W of Piqua, banks of Blue Lick R., *S & Su 9594*.

*S. sempervirens* L. var. *mexicana* (L.) Fern. $2n = 9_{II}$. **North Carolina.** Beaufort Co.: S of Washington, just S of Pamlico R., *S & Su 9749*. $2n = 18$. **Florida.** Walton Co.: Freeport, US-331 just N of FL-20, *S & Su 10133*.

*S. sempervirens* L. var. *sempervirens*. $2n = 18$. **Massachusetts.** Bristol Co.: Somerset, N of town along Segreganset Estuary, *S 9184*.

*S. shortii* Torr. & Gray. $2n = 18$. **Kentucky.** Flemming Co.: S of town of Bluelicks, S banks of Bluelicks R., *S & Su 9598*.

*S. speciosa* Nutt. var. *speciosa*. $2n = 18_{II}$. **South Carolina.**[2] Edgefield Co.: SC-230 17 km N of county line, *S & Su 9817*.

*S. sphacelata* Raf. $2n = 18$. **North Carolina.** Mitchell Co.: W of Bakersville, NC-226 1.5 km W of NC-80, *S & Su 9649*.

*S. stricta* Ait. $2n = 9_{II}$. **North Carolina.**[2] Brunswick Co.: NC-133 W of Wilmington, *S & Su 9763*. $2n = 18$. **South Carolina.** Clarendon Co.: US-521 1.1 km SE of Wilson, *S & Su 9786*. Hampton Co.: US-601 22.4 km S of Hampton, *S & Su 9803*. $2n = 36$. **Louisiana.**[2] St. Tammany Parish: E of LaCombe, US-191 2.4 km E of LA-434, *S & Su 10118*. **South Carolina.**[2] Colleton Co.: NW of Jacksonboro, NC-64 8.7 km from US-17, *S & Su 9801*. **Texas.**[2] Austin Co.: TX-36 4.2 km N of Sealy (Farm Rd.-1094), *S & Su 10071*. Harrison Co.: N of Baytown, vicinity of N. Maine St. exit off I-10, *S & Su 10080*. Orange Co.: NE of Vidor, TX-12 ca. 3 km NE of I-10, *S & Su 10079*. $2n = 54$. **Florida.** Bay Co.: E of Ebro, FL-20 3 km E of FL-79, *S & Su 10138*. Walton Co.: FL-20 3.2 km E of Freeport (US-331N), *S & Su 10134*. **North Carolina.**[2] NNW of Supply, NC-211 13.4 km SSE of Columbus Co. line, *S & Su 9766*. **South Carolina.** Berkeley Co.: NC-17 9.2 km SE of Jamestown (US-17alt.), *S & Su 9796*. Jasper Co.: NW of Ridgeland, SC-652 14.9 km SE of Pineland, *S & Su 9805*.

*S. tortifolia* Ell. $2n = 18$. **Louisiana.**[2] Sabine Parish: N of Many, LA-175 10.7 km N of US-171, *S & Su 10040*. **South Carolina.** Berkeley Co.: SC-45 ca. 5 km E of St. Stephen, Francis Marion Nat'l For., *S & Su 9789*.

*S. uliginosa* Nutt. $2n = 18_{II}$. **Maine.**[2] York Co.: Wells Beach, W of beach front, *S & Su 9590*. **Massachusetts.** Essex Co.: N of Newbury, 1.5 km W of Plum Is. R., opposite airport, *S & Su 9576*. **New Jersey.**[2] Ocean Co.: Tuckerton, coastal cedar marsh E of town centre, *S & Su 9524*. **Rhode Island.**[2] Washington Co.: S of Indian Lake Shores, US-1 4.9 km S of RI-138W, *S & Su 9545*.

*S. ulmifolia* Muhl. ex Willd. $2n = 18$. **Arkansas.** Crawford Co.: US-71 5.8 km S of county line, *S & Su 9964*. Washington Co.: S of Fayetteville, US-71 just S of AR-170, *S & Su 9957*. **Illinois.** Kakankee Co.: NW of Bradley, Kakankee R. State Park, by Rocky R., *S & Su 9870*. Union Co.: Bald Knob Rd. N of Bald Knob, *S & Su 9880, S & Su 9881*. White Co.: S of Norris City, IL-1 1.78 mi N of county line, *S & Su 9426*. **Missouri.** Carter Co.: approx. between Van Buren and Hunter, gravel extension of MO-T 7.8 km SW of US-60, *S & Su 9906*. Douglas Co.: MO-14 at Twin Bridges, woods by N. Fork of

Table 1. Continued.

White R., near MO-181, *S & Su 9930.* Hickory Co.: MO-64B W of Pittsburg, *S & Su 9940.* Oregon Co.: N of Greer, MO-19 16.6 km S of US-60, vicinity of Mark Twain Nat'l For. Rd.-3174, *S & Su 9918, S & Su 9919, S & Su 9920.* Phelps Co.: S of Jerome, Co. Rd.-D at I-44 exit, *S, Su & Ah 9385.* Taney Co.: MO-76 11.8 km W of county line, *S & Su 9934.* Washington Co.: MO-8 6.6 km W of Potosi, *S, Su & Ah 9389.* Wayne Co.: Co. Rd.-F 0.1 km E of US-67 7.8 km S of Greenville, *S & Su 9893*; NE of Wappapello, MO-2 a few km NE of MO-D, *S & Su 9886*; E of Williamsville, MO-49 2.5 km E of Co. Rd.-A, *S & Su 9900.*

*Virgulus ericoides* (L.) Reveal & Keener var. *ericoides.* $2n = 10$. **Illinois.** St. Clair Co.: Fairview Heights, Community Park, bluff of Mississippi R., *S & Su 9408.* **Texas.** Grimes Co.: E of Navasota, TX-105 1.5 km E of Farm Rd.-362, *S & Su 10067.* $2n = 10$. **Texas.** Dallas Co.: N of Cedar Hill, area opposite 1110 Cedar Hill Rd., *S & Su 10006.* $2n = 10 + 0$-3 supernumeraries. **Texas.** Lamar Co.: S of Powderly, US-271 N of Paris, *S & Su 10001.*

*V. oblongifolius* (Nutt.) Reveal & Keener. $2n = 10$. **Nebraska.** Hooker Co.: N of Mullen, bluff of Middle Loop R., just E of NE-97, *S, Su & Ah 9197.* $2n = 20$. **Arkansas.** Logan Co.: Magazine Mt., top of Cameron Bluff, *S & Su 9970.* **Missouri.** Oregon Co.: N of Greer, MO-19 just N of For. Rd.-3188 and Eleven Point R., limestone bluff glade, *S & Su 9921.* Washington Co.: MO-21 NE of Potosi, just N of MO-8, *S, Su & Ah 9398*; MO-8 6.6 km W of Potosi, *S, Su & Ah 9394.*

*V. patens* (Soland. *in* Ait.) Reveal & Keener var. *gracilis* (Hook.) Reveal & Keener. $2n = 5_{II}$. **Texas.** Harrison Co.: NE of Marshall, TX-43 7.2 km NE of US-59, *S & Su 10025.*

*V. patens* (Soland. *in* Ait.) Reveal & Keener var. *patens.* $2n = 20$. **Texas.** Fort Bend Co.: N of Orchard, TX-36 5 km S of county line, N of Farm Rd.-1489, *S & Su 10073.*

*V. patens* (Soland. in Ait.) Reveal & Keener var. *patentissimus* (Torr. & Gray) Reveal & Keener. $2n = 20$. **Missouri.** Bollinger Co.: 1.2 km W of Arab, *S & Su 9885.*

*V. patens* (Soland. *in* Ait.) Reveal & Keener var. *phlogifolius* (Muhl.) Reveal & Keener. $2n = 20$. **Illinois.**[2] Hamilton Co.: 7.5 km E of McLeansboro at Co. Rd.-1400E, *S & Su 9421.* **Kentucky.** Pulaski Co.: KY-461 7 km NE of Shopville, *S & Su 9451.*

sachusetts; *S. patula* Muhl. ex. Willd. var. *strictula* Torr. & Gray, $2n = 9_{II}$ (one population) from Mississippi; and *S. pulchra* Small, $2n = 18_{II}$ (3 populations) from North Carolina. Many of the counts (99) represent the first report(s) for a taxon, or ploidy level of a taxon, for a particular province or state, based on data compiled on nearly 7000 chromosome number reports of North American asters and goldenrods (Semple, 1992): e.g., *Aster puniceus* L. ($2n = 16$) from Georgia, *Heterotheca camporum* (Greene) Shinners

Table 2. Summary of chromosome number reports by genus by area. The numbers of counts representing first report(s) of a taxon, or ploidy level within a taxon, for each region are given as subscripts.

| Region | Total | *Aster* | *Virgulus* | *Euthamia* | *Solidago* | Other Genera |
|---|---|---|---|---|---|---|
| **Canada** | | | | | | |
| Ontario | 9 | $5$ | — | — | $3_1$ | 1 |
| **United States** | | | | | | |
| Alabama | 6 | $4_4$ | — | — | $1_1$ | $1_1$ |
| Arkansas | 11 | $7_4$ | 1 | — | 2 | 1 |
| Connecticut | 1 | $1_1$ | — | — | — | — |
| Florida | 5 | 1 | — | — | 3 | 1 |
| Georgia | 2 | $2_1$ | — | — | — | — |
| Illinois | 25 | 11 | $2_1$ | — | $10_2$ | 2 |
| Indiana | 3 | 2 | — | — | 1 | — |
| Kentucky | 37 | $20_6$ | 1 | — | $16_6$ | — |
| Louisiana | 14 | $6_5$ | — | — | $6_3$ | $2_1$ |
| Maine | 8 | 4 | — | — | $4_1$ | — |
| Massachusetts | 15 | $6_1$ | — | — | $8_2$ | 1 |
| Minnesota | 2 | 2 | — | — | — | — |
| Mississippi | 11 | $6_1$ | — | — | $5_4$ | — |
| Missouri | 35 | $13_4$ | 4 | — | $17_2$ | $1_1$ |
| Nebraska | 4 | — | 1 | — | $3_1$ | — |
| New Jersey | 11 | $5_2$ | — | — | $4_2$ | $2_1$ |
| New York | 1 | — | — | — | 1 | — |
| North Carolina | 49 | $15_1$ | — | — | $26_7$ | $7_1$ |
| Oklahoma | 6 | $6_3$ | — | — | — | — |
| Pennsylvania | 3 | $1_1$ | — | — | $2_1$ | — |
| Rhode Island | 2 | — | — | — | $2_2$ | — |
| South Carolina | 25 | $5_1$ | — | 1 | $17_7$ | $2_1$ |
| South Dakota | 3 | — | — | — | 3 | — |
| Tennessee | 7 | $6_2$ | — | — | $1_1$ | — |
| Texas | 36 | $12_4$ | 4 | 3 | $12_8$ | 4 |
| Wisconsin | 1 | 1 | — | — | — | — |
| TOTALS | $333_{96}$ | $142_{41}$ | $14_1$ | 5 | $147_{51}$ | $25_6$ |

var. *glandulissimum* Semple ($2n = 36$) from Alabama, *Solidago lepida* DC. ($2n = 18$) from Ontario, *S. flexicaulis* L. ($2n = 90$) from Kentucky. *S. fistulosa* Mill. ($2n = 18$) from Alabama, *S. odora* Ait. var. *odora* ($2n = 9_{II}$) from New Jersey and *S. puberula* Nutt. var. *pulverulenta* (Nutt.) Chapm. ($2n = 9_{II}$) from South Carolina. The number of reports and the number of first reports for each province and state are summarized in Table 2 and each case is identified in Table 1. First reports are listed for the fol-

lowing political regions: Alabama, Arkansas, Connecticut, Georgia, Illinois, Kentucky, Louisiana, Maine, Massachusetts, Mississippi, Missouri, Nebraska, New Jersey, North Carolina, Oklahoma, Ontario, Pennsylvania, Rhode Island, South Carolina, Tennessee and Texas.

## ASTER PILOSUS COMPLEX

The *Aster pilosus* Willd. complex includes all of the eastern North American members of *Aster* sect. *Dumosi* Torr. & Gray subsect. *Porteriani* (Rydb.) Semple: *A. depauperatus* (Porter) Fern., *A. parviceps* (Burgess) Mackenzie & Bush, *A. pilosus* var. *pilosus*, *A. pilosus* var. *pringlei* (A. Gray) Blake, and *A. priceae* Britt. Included in Table 1 are 14 counts representing all eastern members of the complex, whose cytogeography was examined in some detail earlier by Semple and Chmielewski (1985). Special note should be taken of the counts for four collections from Missouri hesitantly treated in Table 1 as *A.* aff. *parviceps* and *A.* aff. *pilosus* var. *pringlei*. One specimen (*Semple et al. 9398*) was tetraploid ($2n = 32$) and was from a cedar glade habitat; three collections were hexaploid ($2n = 48$) and also were from cedar glades. The specimens were glabrous to very sparsely pubescent, which is atypical for *A. parviceps*. Some of the glabrous hexaploid individuals were very similar in growth form and general appearance to the octoploid *A. priceae* (Semple et al., 1989), which is endemic to a small region in southern Kentucky (Table 1, *Semple & Suripto 9438* & *9440-1*), central Tennessee and northern Alabama and Georgia, but the Missouri plants had white rays rather than the blue usual for *A. priceae* along with smaller heads and floral parts. Other individuals from the same cedar glades were slightly pubescent. The hexaploid level and glabrous condition is typical of *A. pilosus* var. *pringlei*, which is not previously reported for the Ozark region. Tetraploids are unknown in var. *pringlei*. Thus, the four collections from Missouri do not fit well into any of the three taxa to which they might be assigned. They cannot be hybrids between *A. pilosus* and another species in a different section or subsection because they have phyllaries and lower stem and rosette leaves typical of the subsection; these traits are modified in hybrids. Following Steyermark (1963), the collections could be assigned to *A. pilosus* var. *demotus* Blake, but the type of this

taxon is just a robust var. *pringlei* from southeastern Virginia (Semple and Chmielewski, 1985). If the collections are determined to be more correctly assigned to *A. pilosus* var. *pringlei* than to *A. parviceps,* then the range of the former must be expanded to include disjunct populations in the northern Ozarks, and one of these would be the only known tetraploid member of the variety. A more definitive way of distinguishing members of the complex is needed than the usual approach based on head and floret size and the degree of upper stem pubescence, because these break down in the case of these glabrous-glabrate Missouri plants. The circumscription of either *A. parviceps, A. pilosus* var. *pringlei* or *A. priceae* will have to be modified to accommodate these cedar glade individuals. A detailed multivariate morphometric analysis is being undertaken to resolve the problem.

## SOLIDAGO STRICTA COMPLEX

The *Solidago stricta* complex in the southeastern United States includes *S. austrina* Small, *S. flavovirens* Chapm., *S. gracillima* Torr. & Gray, *S. perlonga* Fern., *S. pulchra* Small, and *S. stricta* Ait. Cronquist (1980) distinguished individual species on the basis of rhizome, capitulescence and capitulum traits. *Solidago stricta* was distinguished by its elongate, stoloniferous rhizomes, which are lacking in *S. pulchra* and *S. gracillima* (including *S. austrina, S. flavovirens,* and *S. perlonga*). *Solidago pulchra* and *S. gracillima* were distinguished on the basis of stem height, the number of heads, and the number of florets per head; the widely distributed *S. gracillima* was tall with few florets per head, and the narrowly distributed *S. pulchra* was short with a few heads with many florets per head. Radford et al. (1968) treated the complex differently, merging *S. austrina* and *S. pulchra* into *S. stricta,* and they noted that the rare, narrowly distributed *S. gracillima* with more widely spreading capitulescence branches might be conspecific with *S. stricta.*

Three diploid, two tetraploid and three hexaploid reports ($2n = 18$, $2n = 36$, and $2n = 54$, respectively) have been published previously for members of the complex (Beaudry, 1963; Semple et al., 1981, 1984). With the addition of 17 counts for members of the complex reported here in Table 1, a tentative geographic pattern can be recognized now in *S. stricta. Solidago stricta* was

found to be diploid in North and South Carolina, tetraploid in South Carolina, Florida, Louisiana and Texas, and hexaploid in New Jersey, North and South Carolina, and Florida. Thus, the western portion of the range (in the United States at least) is apparently occupied only by tetraploids, but from the Florida Panhandle northward all three ploidy levels may be encountered, with the hexaploid level being most frequently reported to date.

Only a few counts have been reported for other members of the complex. For *Solidago austrina,* there is one diploid report (North Carolina, Beaudry, 1963) and one hexaploid report published as "*S. stricta* (= *S. austrina*)" (North Carolina, Semple et al., 1984). The latter is probably just *S. stricta,* not *S. austrina.* Two diploid reports are known for *S. gracillima* (Alabama, Beaudry, 1963; South Carolina, Table 1 here).

*Solidago pulchra* (*sensu* Cronquist) is known from only a few coastal counties in North and South Carolina and was previously unknown cytologically. It was found to be tetraploid ($2n = 18_{II}$) at three populations in separate counties in North Carolina (Table 1). Our plants were clearly different from any of the *S. stricta* collections, being much shorter, having heads with a campanulate-hemispherical versus cylindrical shaped involucres and bright yellow versus yellow-green phyllaries, and more ray and disc florets per head. Differences in habitat preference may also exist, but a number of our collections came from disturbed areas whose original character was unclear; additional data are needed to clarify this distinction.

Because stem height in goldenrods is a very plastic trait and because ploidy level is known to influence involucre height and the numbers of florets per head (Beaudry and Chabot, 1957; Beaudry et al., 1958; Beaudry, 1960, 1970; Melville and Morton, 1982; Heard and Semple, 1988; Semple et al., 1990), separating taxa in the *S. stricta* complex on the basis of these traits may not lead to a useful classification. It is clear from the chromosome counts now reported that at least one of the taxa in the complex includes more than one ploidy level and that diploids in all the taxa occur on the coastal plain in the Carolinas. A detailed cytogeographic and multivariate morphometric analysis of the complex is needed to determine the distribution of cytotypes throughout the range of each taxon and to determine how many of these taxa warrant recognition.

## SOLIDAGO ULIGINOSA

The cytogeography of *Solidago uliginosa* was examined by Chmielewski et al. (1987), who reviewed previous reports (Beaudry et al., 1958; Beaudry and Chabot, 1959; Beaudry, 1969; Kapoor, 1970, 1977; Morton, 1981; Semple, 1981; Semple et al., 1981, 1984; Löve and Löve, 1982; Chmielewski, 1985). In those studies, diploids were common across the range of the species in eastern Canada and the northeastern United States. In contrast, tetraploids were reported from several disjunct areas: limestone pavements around northern Lake Huron in Ontario (five sites) and northern Lake Michigan in Michigan (two sites), near James Bay in northwestern Québec (Beaudry, 1969; one site), west of Montréal in southern Québec (Beaudry, 1969; one site) and the northeastern United States (Beaudry and Chabot, 1959; one site each in eastern Massachusetts and southeastern Pennsylvania; Beaudry, 1963; one site each in central Massachusetts and northern West Virginia). Since 1988 two additional diploid counts have been reported (Semple et al., 1989). To these previous reports we add four tetraploid counts here (Table 1; one each from near the coast in New Jersey, Rhode Island, Massachusetts, and Maine). To date, all counts from the southeastern portion of the species's range are tetraploid. Thus, tetraploids are the dominant cytotype in two disjunct areas (one east and one west of the Appalachian Mountains) and occur rarely in several other parts of the range. Diploids are unknown in the southeastern portion of the range of the species.

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# INTRASPECIFIC TAXONOMY AND COMPARISONS OF NRDNA ITS-2 SEQUENCES OF *ARISAEMA RINGENS* (ARACEAE)

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**ABSTRACT**

The second internal transcribed spacer (ITS-2) of ribosomal DNA (rDNA) was sequenced for the three phenotypes of *Arisaema ringens* (Araceae). These sequences were invariant, and are therefore not systematically informative. However, when considered along with the anatomical, morphological, cytological, and palynological data summarized here, the recognition of intraspecific taxa in *A. ringens* is not supported.

Key Words: *Arisaema*, nrDNA, ribosomal DNA, transcribed spacer, ITS-2

## INTRODUCTION

*Arisaema ringens* (Thunberg) Schott (section Pistillata; Araceae), Japan, China and S. Korea, was divided by Engler (1879) into two varieties, *α sieboldii* and *β praecox,* based on cataphyll and petiole color. The former has green cataphylls and pale violet petioles, and the latter has red cataphylls and pale green petioles. Workers have had varying opinions of these taxa. Palibin (1901) and Chung (1957) agreed with Engler in maintaining two varieties. Other taxonomists have viewed these phenotypes as different species (e.g., De Vriese, 1839; Nakai, 1952) or, more recently, united them into a single species (e.g., Ohwi and Kitagawa, 1983; Ohashi and Murata, 1980; Wu and Li, 1979). Koyama (1984) made Engler's varieties into forms based on spathe color rather than cataphyll and petiole color, i.e., *A. ringens* f. *sieboldii* with dark purple spathes and *A. ringens* f. *praecox* with greenish spathes. Ko and Kim (1985) agreed with Koyama.

In the field three phenotypes of *Arisaema ringens* are found. Based on the current intraspecific taxonomy, these phenotypes may be separated as follows: individuals with purple spathe margins and petioles [var. *sieboldii* (de Vriese) Engl.], individuals with purple spathe margins and green petioles [var. *praecox* (de Vriese)

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Engl.], and individuals with greenish spathe margins and green petioles (f. *praecox* T. Koyama). If, however, petiole color is recognized as a good taxonomic character, then characters of var. *sieboldii* and var. *praecox* are found within f. *sieboldii*.

Several recent studies have examined the intraspecific systematics of *Arisaema ringens*. Morphology and geographical distribution are treated in Ko and Kim (1985). Cytology, anatomy and palynology have also been studied (Ko et al., 1990; Oh et al., 1990; Ko et al., 1987; Ko and Kim, 1985; Hotta, 1971; and Ito, 1942). In order to further clarify the intraspecific relationships in *A. ringens* we examined the sequence of one of the internal spacers of large subunit rDNA (ITS-2). DNA sequences have proved extremely useful in other taxonomic studies (Crawford, 1990). The coding regions of rDNA (18S, 5.8S, and 28S) are not useful at the intraspecific level because they evolve very slowly in sequence and almost not at all in length. These sequences are particularly useful at the level of family and above (Baverstock and Johnson, 1990; Schaal and Learn, 1988). The intergenic spacer (IGS) evolves rapidly both in sequence and length, making it difficult to use except at the population level (Learn and Schaal, 1987; Jorgensen and Cluster, 1988). The ITS regions (ITS-1 and ITS-2), however, have an intermediate level of variation (Baldwin, 1992a; Schaal and Learn, 1988; Hamby and Zimmer, 1992) that makes them ideal for use at or below the generic level. No studies have reported ITS sequences at the subspecific level; at the specific level, percent sequence divergence ranges from 0.4% to 12.9%, excluding the single value of 0% for variation within *Madia bolanderi* (Baldwin, 1992a).

## METHODS

Plants were grown in the Washington University greenhouse from corms collected in the Jeon-La-Nam-Do Province of Korea. Plants with purple spathes and purple petioles and peduncles were from near Dae-Heung Temple, Hae-Nam Kum. Plants with green or purple spathes and green petioles and peduncles were from Kun-Oe Myun, Wan-Do (Island) Kun. DNA was extracted from fresh tissue using the CTAB procedure of Doyle and Doyle (1987) with the addition of a phenol extraction. Primers "ITS-3" (GCATCGATGAAGAACGTAGC) and "ITS-4" (TCCTCCGCTTATTGATATGC) for PCR amplification of ITS-2 were

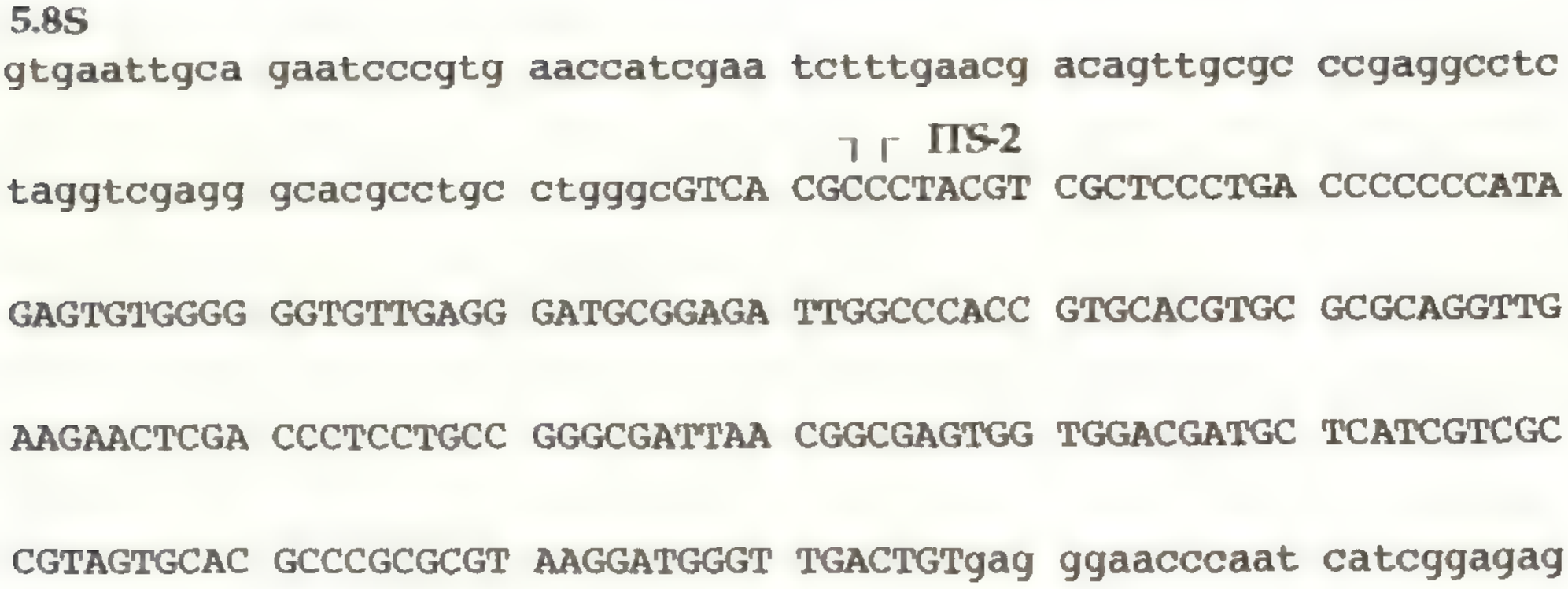


Figure 1. Nucleotide sequence of the rDNA ITS-2 region of the three phenotypes of *Arisaema ringens* including the 28S rDNA flanking region and most of the 5.8S rDNA. Overlap sequence from primers 3 and 4 is indicated in capitals.

constructed from the consensus sequences reported by White et al. (1990). The fourth base (C) from the 5′ end of primer "ITS-3" was changed to T to match the sequences for flowering plants reported elsewhere (e.g., Yokata et al., 1989). Both strands of the double stranded PCR products were directly sequenced using Sequenase (US Biochemicals). Sequence overlap was obtained for 52.5 percent of the total sequence and 75.4 percent of ITS-2 (Figure 1). Sequencing protocols are essentially those given by US Biochemicals except that labeling and extension reactions were performed in a single step, Sequenase was diluted 1:6 rather than 1:8, and termination reactions were carried out at 49°C. The entire sequence of ITS-2 and most of the 5.8S rDNA was sequenced for one individual of each phenotype.

## RESULTS

The sequences obtained for the three phenotypes were identical, indicating to us that no further sequences need be sampled for *Arisaema ringens,* especially as the three samples are from two different locations. ITS-2 was found to be 244 bases long with a G+C content of 61.5 percent (Figure 1). These values are similar to other reported ITS-2 sequences (Yokata et al., 1989; Kavanagh and Timmis, 1988; Takaiwa et al., 1985). The location of the ends of the 5.8S and 26S sequences are based on comparisons

Table 1. Summary of characters of *Arisaema ringens* var. *praecox,* var. *sieboldii,* and f. *praecox.*

| | Taxon | | |
|---|---|---|---|
| | var. *praecox* | var. *sieboldii* | f. *praecox* |
| Morphology | | | |
| Peduncle | green | purple | green |
| Petiole | green | purple | green |
| Spathe | purple | purple | green |
| Cytology[1] | | | |
| Chromosome no. ($2n$) | 28 | 28 | — |
| Karyotype | | | |
| Relative size | | | |
| Very long | 1 | 1 | — |
| Long | 9 | 8 | — |
| Medium | 1 | 2 | — |
| Small | 3 | 3 | — |
| Total chromosomal length ($\mu$m) | | | |
| Ave. | 6.57 | 3.31 | — |
| Range | 3.95–8.83 | 2.07–4.35 | — |
| Type | | | |
| Metacentric | 2 | 3 | — |
| Submetacentric | 12 | 10 | — |
| Subtelocentric | 0 | 1 | — |
| Anatomy—Cell wall specialization index[2] | | | |
| Peduncle | 2.10 | 1.50 | |
| Petiole | 3.75 | 2.90 | — |
| Root | 3.90 | 4.85 | — |
| Ave. | 3.25 | 3.08 | — |

[1] Ko, S. C. & Y. S. Kim, 1985.
[2] Ko, S. C. et al., 1990.

with published ITS-2 sequences (Rathgeber and Capesius, 1989; Yokata et al., 1989; Kavanagh and Timmis, 1988; Kiss et al., 1988; Takaiwa et al., 1985).

## DISCUSSION AND CONCLUSIONS

The intraspecific taxonomy of *Arisaema,* as noted previously, is currently confused, especially so if we wish to recognize the three variable but non-overlapping phenotypes recognizable in the field. In addition the names of these phenotypes are non-heirarchical, i.e., var. *praecox,* var. *sieboldii,* and f. *praecox.* Table 1 summarizes the anatomy, cytology, and morphology of the

intraspecific taxa of *Arisaema ringens*. *Forma praecox* has not been the subject of previous studies other than morphology.

Cytologically, *Arisaema ringens* var. *praecox* and var. *sieboldii* are very similar, both having $2n = 28$ chromosomes and nearly identical karyotypes (Table 1). Although they share a pair of chromosomes that is slightly different from one another in length and chromosome type, these differences are somewhat subjective, e.g., chromosome length is dependent on tissue condition and age of tissue as well as parameters of staining. Geographically these taxa occur in the same subtropical to warm temperate region. Although electron density of the pollen ektexine of var. *sieboldii* is somewhat greater than in var. *praecox*, there are no significant differences in pollen size, shape, and wall architecture. Cross-sections of roots, petioles, petiolules, peduncles, and leaves show the same tissue arrangement and level of tissue specialization and differentiation in both taxa. Diameter and cell wall thickness of tracheids, and diameter and length of fibers in both taxa are not significantly different, and these characters have been shown not be phylogenetically useful in *Arisaema* (Ko et al., 1990). Based on the level of specialization of cell wall thickenings, var. *sieboldii* is slightly more advanced in its root anatomy and var. *praecox* is slightly more advanced in areal organs. Although the distribution of colors of peduncle, petiole, and spathe are not overlapping, they are quite variable within a given taxon.

Many morphological characters of plants, some of them quite striking, have been shown to be under the control of alleles of one or a few genes (Coen and Meyerowitz, 1991; Gottlieb, 1984; Hilu, 1983). It is probable that colors thought to distinguish intraspecific taxa of *Arisaema ringens* are similarly controlled and represent intraspecific polymorphism rather than synapomorphies of evolutionary lineages. Sequences of ITS-2 show no differences among the intraspecific taxa of *Arisaema ringens*. These sequences are known to be good markers of evolutionary lineages at or near the species level (Baldwin, 1992b; Baldwin et al., 1992; Suh et al., 1992). Insignificant difference in morphology and anatomy, and the lack of ITS-2 sequence variation, suggests that the intraspecific taxa of *Arisaema ringens* should be consolidated and a single polymorphic taxon should be recognized. Further work is required to assay levels of ITS-2, as well as ITS-1, variation within and among other species of *Arisaema*.

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# *ANTENNARIA PULVINATA* GREENE: THE LEGITIMATE NAME FOR *A. AROMATICA* EVERT (ASTERACEAE: INULEAE)

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## ABSTRACT

Canonical variates analysis was used as an analytical technique to document morphological discontinuities among individuals of *Antennaria media* ($n = 63$), *A. pulvinata* ($n = 103$), *A. rosea* ($n = 64$) and *A. umbrinella* ($n = 65$). Evaluation of the defined classification criterion indicated that 94% of the specimens were classified correctly. The classification criterion was subsequently used to classify type collections of *A. aromatica* ($n = 26$) into one of the previously defined groups. Results based on these analyses as well as previously published information demonstrate that *A. aromatica* and *A. pulvinata* are morphologically indistinguishable. The analyses also indicate that *A. pulvinata* and *A. rosea* exhibit morphological integrity relative to each other and would best be treated as distinct species. The four species, *A. media, A. pulvinata, A. rosea* and *A. umbrinella,* exhibit morphological integrity and should be treated as distinct. A list of synonymy is provided for *A. pulvinata.*

Key Words: *Antennaria media, A. pulvinata, A. rosea, A. umbrinella, A. aromatica*

## INTRODUCTION

*Antennaria aromatica* Evert was originally described as a sexual diploid Cordilleran species (Evert, 1984). Subsequent studies have demonstrated that the species is morphologically, cytologically and reproductively more variable (Bayer and Stebbins, 1987; Bayer, 1984, 1989a), as well as more widely distributed (Chmielewski and Chinnappa, 1988a; Bayer, 1989a), than initially proposed. Additional interest in *A. aromatica* stems from the implication that the species is one of the progenitors of the *A. rosea* Greene polyploid complex, specifically, that entity described as *A. rosea* subsp. *pulvinata* (Greene) R. Bayer (Bayer, 1989b).

Evert (1984) was able to differentiate *Antennaria aromatica* from both *A. media* Greene and *A. umbrinella* Rydberg, other members of the complex, by its copious and persistent glandulosity, widely cuneate-spatulate basal leaves and distinctive citronella-like odor. Bayer (1989b) concluded that his subsp. *pulvinata* resembled *A. aromatica,* except in that it lacked glandular hairs. Although Greene (1898) described both "female" and "male" specimens of *A. pulvinata,* Bayer (1989b) concluded that his subsp. *pulvinata* is entirely pistillate, apomictic and polyploid.

*Antennaria aromatica* was initially considered endemic to southwestern Montana and adjacent parts of Idaho and Wyoming occupying limestone talus and xeric habitats (Evert, 1984). The species was subsequently reported from Alberta, British Columbia and California (Chmielewski and Chinnappa, 1988a). Bayer (1991) rejected the latter range extension, citing specimen misidentification, as determined by either inspection or deduction, and instead supported the distribution for the species presented by Bayer (1989a).

Although *Antennaria aromatica* was originally described as an endemic, morphologically uniform, sexual diploid species, five years later it was more appropriate to consider the species as wider ranging (Chmielewski and Chinnappa, 1988a; Bayer 1989a), reproductively variable (either sexual or apomictic) and cytologically variable (diploid, tetraploid or hexaploid) (Bayer and Stebbins, 1987; Bayer 1989a). Reproductive biology, hybridization, polyploidization and dioecism have all contributed to morphological intergradation among species of *Antennaria* and thereby magnified the present state of confusion not only in this species but also the genus (Fernald, 1950; Cronquist, 1955; Anderson, 1959; Hultén, 1968; Welsh, 1974; Scoggan, 1979; Porsild and Cody, 1980; Moss, 1983).

This investigation incorporates the results of a phenetic study of gross morphology with information published during the past decade to determine whether it is possible to distinguish consistently and confidently among *Antennaria aromatica, A. media, A. pulvinata* (including subsp. *albescens* E. Nelson), *A. rosea* and *A. umbrinella.* Having established those taxa which are distinct, some comments are offered concerning the presumed evolutionary history of the group.

## MATERIALS AND METHODS

Herbarium specimens, including type material, utilized in the phenetic study were borrowed from ALTA, ARIZ, CAN, COLO, DAO, F, LEA, MO, MONT, MOR, MT, NY, OS, PH, RM, SLRO, UAC, UBC, UC, US, WIN and WS (Holmgren et al., 1990). Specimens of each species were selected on the basis of completeness and comparability in terms of developmental stage. Only mature pre-dehiscent specimens were included. These specimens reflect a range in plant size,

Table 1. Morphological characters included in the phenetic study of *Antennaria aromatica, A. media, A. pulvinata, A. rosea* and *A. umbrinella.*

| Structure | Character |
|---|---|
| Vegetative | Basal leaf length (mm): BASALLL<br>Basal leaf width (mm): BASALLW |
| Vegetative-Reproductive | Plant height (mm): HEIGHT<br>Number of cauline leaves: NOCAULL<br>Cauline leaf length (mm): CAULLL<br>Cauline leaf width (mm): CAULLW<br>Number of capitula: NOCAP<br>Involucre height (mm): INVOHT<br>Outer phyllary length (mm): OUTPHYL<br>Outer phyllary width (mm): OUTPHYW<br>Inner phyllary length (mm): INNPHYL<br>Inner phyllary width (mm): INNPHYW |
| Reproductive | Pappus length (mm): PAPPUSL<br>Corolla length (mm): COROLLAL |

involucre size, habit and provenance. No *a priori* restrictions were placed on the total number of specimens considered necessary to represent the range of morpho-geographic variation within each species. Herbarium specimens ($n = 295$) were identified prior to analysis as *Antennaria aromatica* ($n = 26$ type sheets), *A. media* ($n = 63$), *A. pulvinata* ($n = 103$), *A. rosea* ($n = 64$) and *A. umbrinella* ($n = 65$). Qualitative characters used to identify the specimens to species prior to analysis included habit, degree of pubescence, color, shape and texture of the phyllaries, exsertion of the style and the presence or absence of papillae on the achenes. These characters were not utilized in the phenetic study. Both pistillate and staminate plants were included in the phenetic study.

Data were collected for 14 quantitative characters for each specimen (Table 1). These characters were selected primarily because they were uncorrelated ($|r| < .70$), described the general form of vegetative and reproductive structures, were not used directly in the classification of individuals to *a priori* groups, were not ipsative and were previously shown to be useful in differentiating among species of *Antennaria* (Chmielewski and Chinnappa, 1988b, 1991; Chmielewski et al., 1990a, 1990b). Several of these characters, including plant height, leaf shape, number of capitula, size of capitula and floret size, are typically used to differentiate among species of *Antennaria.* The data matrix contained no missing values.

Canonical variates analysis was facilitated with the SAS (SAS Institute Inc., 1989) DISCRIM (crossvalidate and posterr options) and CANDISC procedures. To meet the assumptions of multivariate normality (Gilbert, 1968), length measurements were transformed to their logarithms (base 10) and count data were transformed to their square roots prior to initiating multivariate analysis. Classificatory discriminant analysis was used to classify specimens of *Antennaria media, A. pulvinata, A. rosea* and *A. umbrinella,* defined *a priori* on one or more characters that were not included in the analysis, to species. Correct classification rates and Geisser assignment probabilities were used as indicators of separation among the groups. Tests for equality of group centroids were performed as part of the canonical analysis. The same data set was used to both define and evaluate the classification criterion. The classification criterion was subsequently used to classify the type collections of *A. aromatica* ($n = 26$) into one of the previously defined species. *Antennaria aromatica* was not treated as a separate *a priori* group in the discriminant analysis because the importance of glandularity in the separation of *A. rosea* subsp. *pulvinata* from *A. aromatica* was in my estimation overemphasized. The copious glandularity that is evident on the holotype is less pronounced to lacking on some of the other type collections. Additionally, some specimens that superficially appear non-glandular do possess glands beneath the tomentum. Thus, *A. aromatica* is not considered to be consistently glandular. Trivariate plots of the canonical variate scores were used to facilitate visualization of the results of the multidimensional analysis (DeltaPoint Inc., 1992). Mean value ± standard deviation was determined for each character for each species.

## RESULTS

Canonical variates analysis (CVA) of 14 quantitative morphological characters was used to document discontinuities among specimens of *Antennaria media, A. pulvinata, A. rosea* and *A. umbrinella.* Evaluation of the classification criterion indicated that 94% of the specimens were classified correctly (Table 2). Geisser assignment probabilities were generally greater than .98 for the 278 correctly assigned specimens. The low error count, in conjunction with the high Geisser assignment probabilities, in-

Table 2. Classification summary by number of observations and percent classified into species for the discriminant analysis.

| | Number of Observations and Percent Classified into Species | | | |
|---|---|---|---|---|
| From Species | *media* | *pulvinata* | *rosea* | *umbrinella* |
| *media* | 54 | 8 | 0 | 1 |
| | 85.71 | 12.70 | .00 | 1.59 |
| *pulvinata* | 6 | 97 | 0 | 0 |
| | 5.83 | 94.17 | .00 | .00 |
| *rosea* | 1 | 0 | 63 | 0 |
| | 1.56 | .00 | 98.44 | .00 |
| *umbrinella* | 0 | 1 | 0 | 64 |
| | .00 | 1.54 | .00 | 98.46 |

dicates that classification of additional specimens, that is, type collections of *A. aromatica,* through the use of the classification criterion, would yield acceptable results.

The first and second discriminant functions accounted for 90.5% (73.1 and 17.4% respectively) of the total variation (eigenvalues of 4.263 and 1.015 respectively) among specimens. Ordination of the 295 specimens by canonical analysis is presented as a series of trivariate plots (Figure 1) in which mean canonical scores are indicated for each species. The Mahalanobis distance between groups and associated F-value indicate the group centroids were significantly different ($P < .0001$). The canonical correlation of the first discriminant function (.900), or that squared as the proportion of the variance in the function explained by the four groups (.810), indicates high to moderate correlation with the groups. A strong relationship between the specific linear combination of variables, the canonical variables and the groups is indicated.

Descriptive statistics (mean ± standard deviation) are used to identify character discontinuities for the predefined groupings of specimens (Table 3). Except for STEMHT, NOCAULL, CAULLL, BASALLL, NOCAP and INNPHYW which exhibited moderate to no overlap among all or some of the groups, the remaining characters consistently intergraded among the groups. These characters had the highest loadings on the first canonical axis.

Type specimens of *Antennaria aromatica* were classified, through the use of the classification criterion, to either *A. media* (7%, $n =$

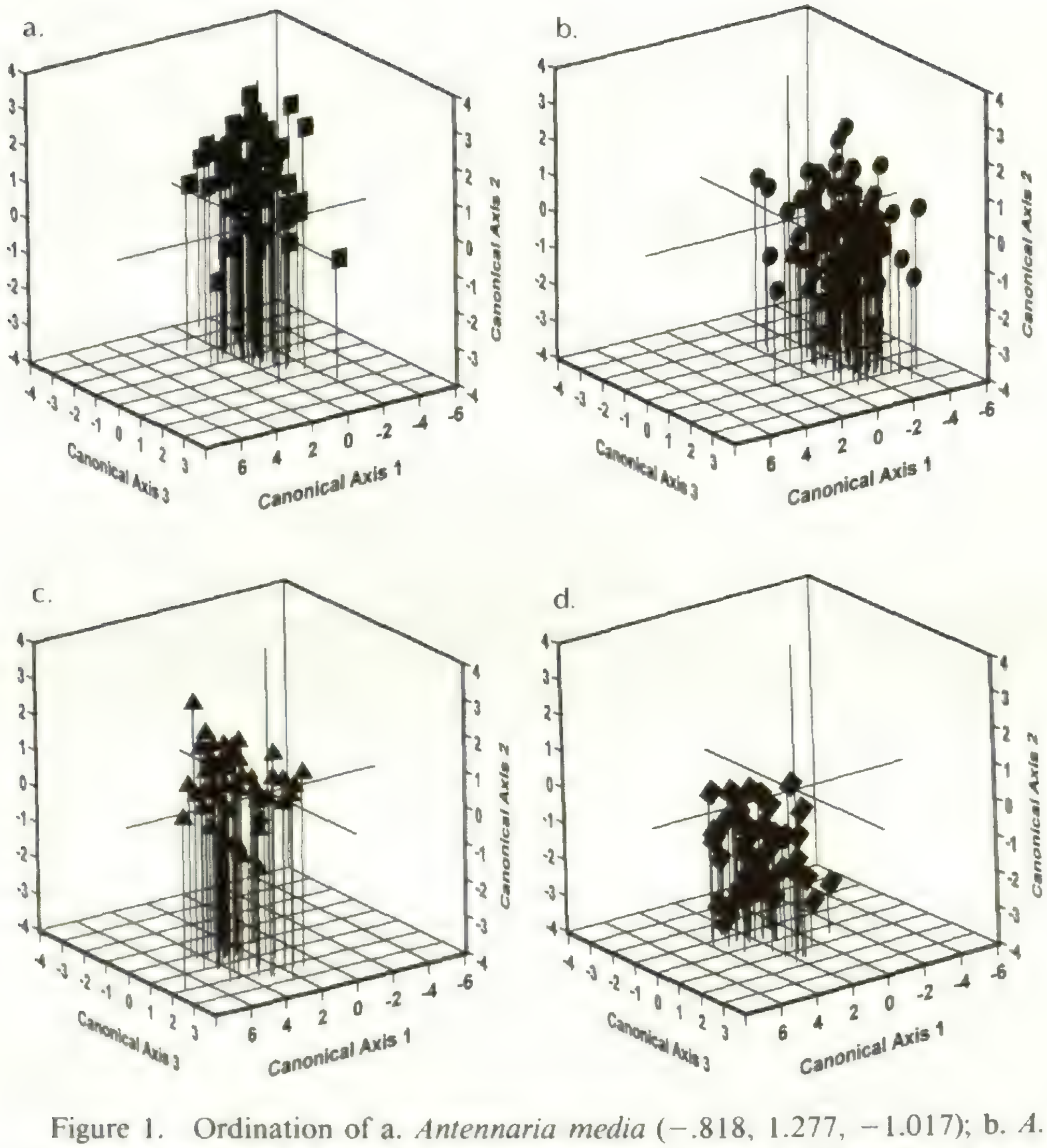


Figure 1. Ordination of a. *Antennaria media* (−.818, 1.277, −1.017); b. *A. pulvinata* (−2.238, −.302, .564); c. *A. rosea* (2.908, .754, .750); and d. *A. umbrinella* (1.476, −1.502, −.646). Group centroids are shown in parentheses (canonical axes 1, 2 and 3 respectively).

2) or *A. pulvinata* (92%, $n = 24$). Geisser assignment probabilities were typically greater than .95 for these specimens.

## DISCUSSION

In describing *Antennaria aromatica,* Evert (1984) noted that the species was morphologically uniform throughout its range. Subsequent comparison of the holotype to average species values via a mean similarity matrix employing Pearson product-moment correlation coefficients (*see* Bayer, 1988a, Table 1) indicated that

Table 3. Summary of mean value ± standard deviation for each of the taxa included in the phenetic study.

| Character | Taxon | | | | |
|---|---|---|---|---|---|
| | *aromatica* | *media* | *pulvinata* | *rosea* | *umbrinella* |
| STEMHT (cm) | 3.12 ± 1.46 | 5.98 ± 2.63 | 5.11 ± 2.61 | 19.81 ± 8.55 | 10.26 ± 3.95 |
| NOCAULL | 5.42 ± 1.68 | 6.65 ± 1.99 | 6.56 ± 1.82 | 12.25 ± 3.31 | 8.49 ± 2.09 |
| CAULLL (mm) | 8.23 ± 2.23 | 11.43 ± 3.18 | 9.93 ± 2.48 | 21.18 ± 6.26 | 11.96 ± 2.91 |
| CAULLW (mm) | 1.87 ± 0.63 | 1.71 ± 0.52 | 1.80 ± 0.48 | 2.25 ± 0.84 | 1.82 ± 0.53 |
| BASALLL (mm) | 8.25 ± 2.04 | 12.07 ± 3.62 | 8.72 ± 2.89 | 17.13 ± 5.40 | 10.31 ± 3.18 |
| BASALLW (mm) | 4.28 ± 1.20 | 3.33 ± 0.96 | 4.15 ± 1.16 | 3.98 ± 1.29 | 3.49 ± 0.83 |
| NOCAP | 3.42 ± 0.99 | 5.00 ± 1.49 | 4.44 ± 1.31 | 12.16 ± 7.79 | 8.20 ± 3.27 |
| INVOHT (mm) | 5.32 ± 0.79 | 5.58 ± 0.66 | 5.93 ± 0.85 | 5.68 ± 0.71 | 4.78 ± 0.73 |
| OUTPHYL (mm) | 3.74 ± 0.79 | 3.90 ± 0.64 | 4.04 ± 0.68 | 3.81 ± 0.64 | 3.28 ± 0.54 |
| OUTPHYW (mm) | 1.20 ± 0.21 | 1.23 ± 0.24 | 1.38 ± 0.25 | 1.09 ± 0.23 | 1.05 ± 0.20 |
| INNPHYL (mm) | 4.87 ± 0.74 | 5.08 ± 0.61 | 5.35 ± 0.68 | 5.07 ± 0.65 | 4.15 ± 0.62 |
| INNPHYW (mm) | 1.03 ± 0.33 | 0.77 ± 0.21 | 0.90 ± 0.24 | 0.48 ± 0.17 | 0.64 ± 0.24 |
| PAPPUSL (mm) | 3.86 ± 0.81 | 4.73 ± 0.63 | 4.57 ± 0.72 | 4.43 ± 0.59 | 3.66 ± 0.52 |
| COROLLAL (mm) | 3.54 ± 0.51 | 3.57 ± 0.57 | 3.83 ± 0.64 | 3.40 ± 0.51 | 2.80 ± 0.53 |

it is "atypical of the species, consisting of really small diploids that do not occur on limestone talus" (Bayer, pers. comm. 1989). Examination of available type material ($n = 26$) indicated that *A. aromatica,* like most *Antennaria* (Chmielewski and Chinnappa, 1988b, 1991; Chmielewski et al., 1990a, 1990b), is indeed variable, exhibiting different degrees of plasticity, with respect to basal leaf length and width, plant height, cauline leaf length and width, degree of pubescence, glandularity and involucre height. *Antennaria aromatica* is therefore a species which illustrates that the nomenclatural type is not necessarily the most typical or representative element of the taxon; it is merely that element with which the name is permanently associated (Lanjouw et al., 1966).

Initially described as a diploid species (Evert, 1984), *Antennaria aromatica* was subsequently reported to include both tetraploid and hexaploid individuals (Bayer, 1984, 1989a; Bayer and Stebbins, 1987). Apparently some confusion exists with respect to the identification of the tetraploid specimen designated CO-458 (Bayer and Stebbins, 1987), as it was included with both *A. aromatica* (toward *A. media*) and *A. rosea* (toward *A. aromatica*) by the authors. This confusion notwithstanding, it is likely that the diploid and polyploid states possessed by individuals of the species have contributed, at least in part, via the gigas effects of polyploidization (Stebbins, 1971) to the observed patterns of plasticity (*see also* Bayer, 1989b) noted above. Because so few cytological determinations are available for the species, statistically valid conclusions pertaining to the relationship between chromosome number and morphology are not possible at this time.

Results based on canonical variates analysis indicate that the degree of morphological overlap among the four taxa, *Antennaria media, A. pulvinata, A. rosea* and *A. umbrinella,* as defined in this study, is minimal. High assignment rates and Geisser assignment probabilities support this conclusion. The conclusion that *A. media, A. rosea* and *A. umbrinella* are morphologically distinct is not a novel one as the species are generally treated as such (*see* Bayer, 1988a, 1988b, 1989c, 1990a; Chmielewski and Chinnappa, 1988b; Chmielewski et al., 1990a, 1990b for discussion). The question remains, how does *Antennaria pulvinata* fit in with these species?

Direct visual comparison of type material indicates that fragments of the holotypes of *Antennaria aromatica* (RM346356) and

*A. pulvinata* (NDG058584) are indistinguishable, as are the paratype of *A. aromatica* (F) and the isotype (CAN105666) and paratype (CAN105674) of *A. pulvinata.*

Although two type collections of *Antennaria aromatica* were originally assigned to *A. media,* through the use of the classification criterion, the 92% success rate observed is in line with the capabilities of the classification criterion as it was defined through the analysis. The classification criterion obtained through canonical variates was initially evaluated at a 94% success rate. Thus, it is unrealistic to expect a higher classification success rate when it is used to classify collections, such as the types of *A. aromatica,* which were not used to define the classification criterion. The analysis demonstrates not only that *A. aromatica* and *A. pulvinata* are indistinguishable but also that morphological intergradation among species of *Antennaria* is a facet of reality.

In attempting to clarify the confusion that surrounds the identity of *Antennaria pulvinata,* Bayer (1989a) concluded that it resembles *A. aromatica* closely, except that it lacks glandular hairs. This character is not infallible however, as glandularity, even among type collections of *A. aromatica,* ranges from a dense cover to trace amounts or even lacking. Additionally, some specimens that superficially appear non-glandular do possess glands beneath the tomentum. Thus *A. aromatica* is not consistently copiously glandular, but rather variable in this regard.

Inasmuch as *Antennaria pulvinata* and *A. aromatica* are identical, the basis for inclusion of the former in *A. rosea* is elusive. If *A. pulvinata* should be included at some taxonomic rank in the *A. rosea* polyploid complex, as proposed by Bayer (1989b), then the results of canonical variates analysis should support this contention. Support would include lower assignment rates for both taxa, as well as lowered Geisser assignment probabilities. Neither of these scenarios is true however in the present study. In circumscribing *A. rosea,* Bayer (1989b) concluded that subsp. *pulvinata* is entirely pistillate, apomictic and polyploid. This non sequitur is unacceptable however as Greene (1898) described both "female" and "male" specimens of *A. pulvinata.* The protologues of *A. pulvinata* and *A. rosea,* gross morphology of type material and the results of canonical variates analysis, all contribute to support the conclusion that the two taxa are morphologically distinct. The two taxa, *A. pulvinata* and *A. rosea,* do exhibit mor-

phological integrity (see Table 3) and should therefore be treated as distinct. As such, it would be inappropriate to include the former species as an infraspecific subdivision of the latter.

Although originally described as an endemic, morphologically uniform, sexual, diploid species, *Antennaria aromatica* is more appropriately described as wider ranging (Chmielewski and Chinnappa, 1988a; Bayer, 1991), both sexual and apomictic (Bayer, 1989a), diploid and polyploid (Bayer, 1989a) and morphologically variable. Gross morphology of type and non-type material, the Pearson product-moment correlation coefficients presented by Bayer (1988a), the protologues of *A. aromatica* and *A. pulvinata,* the fallibility of using glandularity as a diagnostic character and the results of canonical variates analysis all contribute, to varying degrees, to support the conclusion that *A. aromatica* and *A. pulvinata* are conspecific. The latter specific epithet is deemed the legitimate name for the plant and the former a synonym. A list of synonymy is provided for *A. pulvinata.*

## TAXONOMY

The following key may be used to differentiate among the *Antennaria media, A. pulvinata, A. rosea* and *A. umbrinella.*

A. Plants generally tall, greater than 1 dm, typically 1.5–2.5 dm; cauline leaves long, 1.5+ cm, numerous; basal leaves typically lanceolate, occasionally spatulate-lanceolate, 1.2+ cm long; immature involucres nodding ..... *A. rosea*

A. Plants generally compact, less than 1 dm, typically 0.5–1.0 dm; cauline leaves shorter, <1.5 cm, fewer; basal leaves spatulate, obovate, spatulate-obovate, cuneate spatulate to occasionally oblanceolate, typically <1.2 cm; immature involucres not nodding ..... B

B. Stolons elongate, strongly upsurgent at tips and usually woody; basal leaves tufted about stem; tips of involucral bracts dirty white or light brown ..... *A. umbrinella*

B. Stolons short, not upsurgent; basal leaves not tufted about stem; tips of involucral bracts conspicuously darker than base, brown, green, black ..... C

C. Basal leaves typically spatulate-lanceolate with permanent woolly tomentum; inner bracts narrow, linear, tips usually sharp pointed, acute ... *A. media*

C. Basal leaves widely cuneate-spatulate to occasionally oblanceolate; persistently white tomentose on both surfaces; inner bracts broader, frequently obtuse . . . . . *A. pulvinata*

## LIST OF SYNONYMY

*Antennaria pulvinata* Greene, Pittonia 3: 287, 1898. TYPE: Canada: Alberta, Moose Mtn, Elbow River, Rocky Mountains, June 29, 1897, *J. Macoun 18491.* (HOLOTYPE: NDG058584!; ISOTYPE: CAN105666!). *J. Macoun 18493, 18495, 18498.* (PARATYPES: CAN105675!, CAN105674!, NDG058583!, NDG058584!). *J. Macoun 18492.* (TOPOTYPE: CAN105676!).

*Antennaria rosea* subsp. *pulvinata* (Greene) R. Bayer, Brittonia 41: 59, 1989.

*Antennaria pulvinata* subsp. *albescens* E. Nelson, Proc. U.S. Natl. Mus. 23: 702, 1901. *Antennaria albescens* (E. Nelson) Rydb. Rocky Mts. 917, 1067, 1917. TYPE: United States: Idaho, Texas District, Mount Hops, Salmon River Mountains, Aug 17, 1895, *L. F. Henderson 3870.* (HOLOTYPE: US228762!).

*Antennaria aromatica* Evert, Madroño 31: 109, 1984. TYPE: United States: Montana, Carbon Co., Beartooth Range along Hwy 212, ca. .8 km N of Quad Cr., Aug 5, 1981, *E. F. Evert 3406.* (HOLOTYPE: RM346356!; ISOTYPES: MO3229695!, MOR52039!, UC1509580!). *F. W. Pennell, F. B. Cotner and R. L. Schaeffer 23835.* (PARATYPES: F1576300!, PH853371!). *R. J. Bayer and G. L. Stebbins 8092.* (PARATYPE: OS153623!). *E. F. Evert 1780, 3015, 3420.* (PARATYPES: RM346360!, RM346359!, RM346357). *P. A. Robertson 1110.* (PARATYPE: RM330754!). *G. L. Stebbins and R. J. Bayer 8113.* (PARATYPE: UAC41448!).

The original species description of *Antennaria pulvinata* (Greene, 1898), supplemented by the species description for *A. aromatica* (Evert, 1984), deemphasizing glandularity as a diagnostic character for the latter, adequately reflects the morphology of the former as it was applied at the completion of this study. Species descriptions previously presented for *A. media* (including *A. pulchella* Greene, Bayer, 1990b), *A. rosea* (Chmielewski et al., 1990a) and *A. umbrinella* (Chmielewski et al., 1990a) are deemed accurate and were applied accordingly in this study.

The distributions presented for *Antennaria media* (Bayer, 1990b), *A. pulvinata* (as discussed for *A. aromatica* in Chmielewski and Chinnappa, 1988a), *A. rosea* (Chmielewski and Chinnappa, 1988b) and *A. umbrinella* (Chmielewski et al., 1990a) are considered to accurately represent the ranges of these species as they are presently understood.

## EVOLUTIONARY RELATIONSHIPS

*Antennaria media sensu lato,* considered by some to be one of the more important western species of *Antennaria* (*see* Bayer, 1987a), has been implicated in the hybridization events which resulted in *A. alpina* (L.) Gaertner, *A. parvifolia* Nuttall and *A. rosea.* Additionally, *A. media* is considered to possess a pivotal genome, being partially responsible for *A. parlinii* Fernald overlapping morphologically with A. *neodioica* Greene; *A. neodioica* with *A. parvifolia*; *A. parvifolia* with *A. rosea*; and *A. rosea* with *A. alpina* (Bayer, 1987a). The importance of *A. media* in the evolution of all these taxa is in my estimation overemphasized as these apparent relationships represent speculation based on little or no data.

A recent revision of *Antennaria media sensu lato* led Bayer (1990b) to conclude that the diploid cytotype (*A. pulchella* Greene) should be recognized as distinct from the polyploid cytotypes represented by *A. media.* This conclusion, founded on the results of a phenetic study, warrants discussion. First, although polyploid *A. media* occurs throughout the alpine zone of many western North American mountain ranges, extending from the southwestern United States to the western arctic, only specimens from the southern portion of its distribution were included in the analysis. Second, the data set utilized was incomplete and therefore subject to produce unsupported results (see Chmielewski and Chinnappa, 1992). Third, except for *A. scabra* Greene, the taxa included in the list of synonymy were not utilized in the analysis. Fourth, many additional taxa which were previously included in the complex were excluded without comment from the phenetic study (*A. atriceps* Fernald ex Raup, *A. compacta* Malte, *A. fusca* E. Nelson, *A. maculata* Greene, *A. modesta* Greene, *A. mucronata* E. Nelson, *A. pallida* E. Nelson and *A. stolonifera* A. E. Porsild). Additional taxa which I believe should be considered in a revision of *A. media sensu lato,* but which were placed in synonymy with *A. rosea* (Bayer, 1989b), include *A. chlorantha* Greene, *A. lanulosa* Greene, *A. isolepis* Greene and *A. tomentella* E. Nelson. Fifth, although *A. scabra* was considered most similar to *A. aromatica* based on the results of an average similarity matrix (Bayer, 1988a), Bayer (1990b) failed to address this discrepancy, concluding that it was most similar to *A. pulchella.* Similar discrepancies based on the results of an average similarity matrix (Bayer, 1988a) exist

for *A. austromontana* E. Nelson (most similar to *A. aromatica*), *A. candida* Greene (most similar to *A. umbrinella*) and *A. modesta* (most similar to *A. aromatica*). A phenetic study which includes specimens from throughout the range of *A. media sensu lato* and also incorporates all those taxa which may be part of the complex is necessary before a classification scheme may be legitimately proposed. For the time being it would be prudent to treat these dark green-black phyllaried taxa as members of *A. media sensu lato.*

Bayer (1987b) postulated that *Antennaria rosea* is a polyploid compilospecies, the result of multiple hybridizations among several amphimictic species. Results based on phenetic analyses indicated that *A. aromatica, A. corymbosa* E. Nelson, *A. media, A. microphylla* Rydberg and *A. umbrinella* are the major sexual progenitors of the complex, whereas *A. marginata* Greene and *A. rosulata* Rydberg are minor contributors (Bayer, 1990a). Chmielewski et al. (1990a) questioned the likelihood of such a complicated pattern of hybridization events across sectional boundaries. The latter authors instead stated that phenetic analyses, based on a substantially larger sample of specimens, supported a hybrid origin among *A. corymbosa, A. microphylla* and *A. umbrinella.* Although phenetic analyses have led the aforementioned authors to support different positions relative to the origins of *A. rosea,* isozyme data can be used as independent evidence to support the hypothesis of Chmielewski et al. (1990a), that is, that only *A. corymbosa, A. microphylla* and *A. umbrinella* are among the sexual progenitors of the complex (Bayer, 1989d).

*Antennaria umbrinella,* a member of section Alpinae (Chmielewski et al., 1990c) was recently referred to as a member of section Dioicae (Bayer, 1987b), as well as section Alpinae (Bayer, 1989c). A sexual species, *A. umbrinella* is most similar to *A. pulvinata,* the strongly upsurgent, typically woody stolon tips representative of the former species accounting for morphological divergence between the taxa. The role of this species as one of the progenitors of the *A. rosea* polyploid complex was adequately discussed previously.

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# THREE NEW SPECIES OF THE GENUS *PELEXIA* (ORCHIDACEAE, SPIRANTHINAE) FROM COLOMBIA

DARIUSZ L. SZLACHETKO

**ABSTRACT**

The genus *Pelexia* Poit. ex Lindl. occurs in the tropics and subtropics of both Americas: from Argentina in the south to Mexico and Florida in the north. According to Garay (1982) it contains 67 species. *Pelexia* is distinguishable from closely related *Sarcoglottis* Presl by an "externally observable line of adnation" between ovary and lateral sepals.

While studying herbarium materials from COL, P and S, I found some specimens which did not fit the diagnoses of any previously known species. They are described here for the first time.

Key Words: *Pelexia*, new species, Colombia

**PELEXIA CUNDINAMARCAE**, *sp. nov.* (Figure 1)

Involucrum sub angulo recto ad ovarium incurvatum, tubuloso-convolutum. Calcar saccelliforme, apice angusto, discreto, ad ovario soluto. Auriculae labelli crassae, carnosae, ad unguiem adnatae, epichilio longitudinis aequantes. Hypochilium obovatum, epichilium triangulare, minutum, valde incrassatum.

Roots clustered, fleshy. Stem 210–450 mm tall, 5–6 mm in diameter at base, 2 mm in diameter below inflorescence, erect, rather stout, in the upper part glandular. Cauline bracts 4–5, herbaceous, thin, acute, closely adnate to the stem, longer than internodes, the uppermost reaches the base of the inflorescence, glabrous except the uppermost, which is sparsely glandular in the basal portion. Leaves 3–5, basal; petiole long and narrow, up to 120 mm long; blade 55–95 mm long, 13–30 mm wide, lanceolate, acute, in pressed plants grayish-pale violet on the upper surface, dull red on the lower. Inflorescence 40–115 mm long, 8–20-flowered, lax, subsecund. Flowers medium size, perianth tube forms a right angle with the ovary, spur saccate with narrow projection on apex. Floral bracts 15–22 mm long, lanceolate, acute, longer than ovary, herbaceous, thin, delicate, densely glandular outside. Pedicel 1.5–5 mm long, twisted. Ovary 12–15 mm long, densely glandular. Dorsal sepal 11.5 mm long, 4 mm wide, ovate-lanceolate, acuminate, 3-nerved, glandular outside. Free portion of

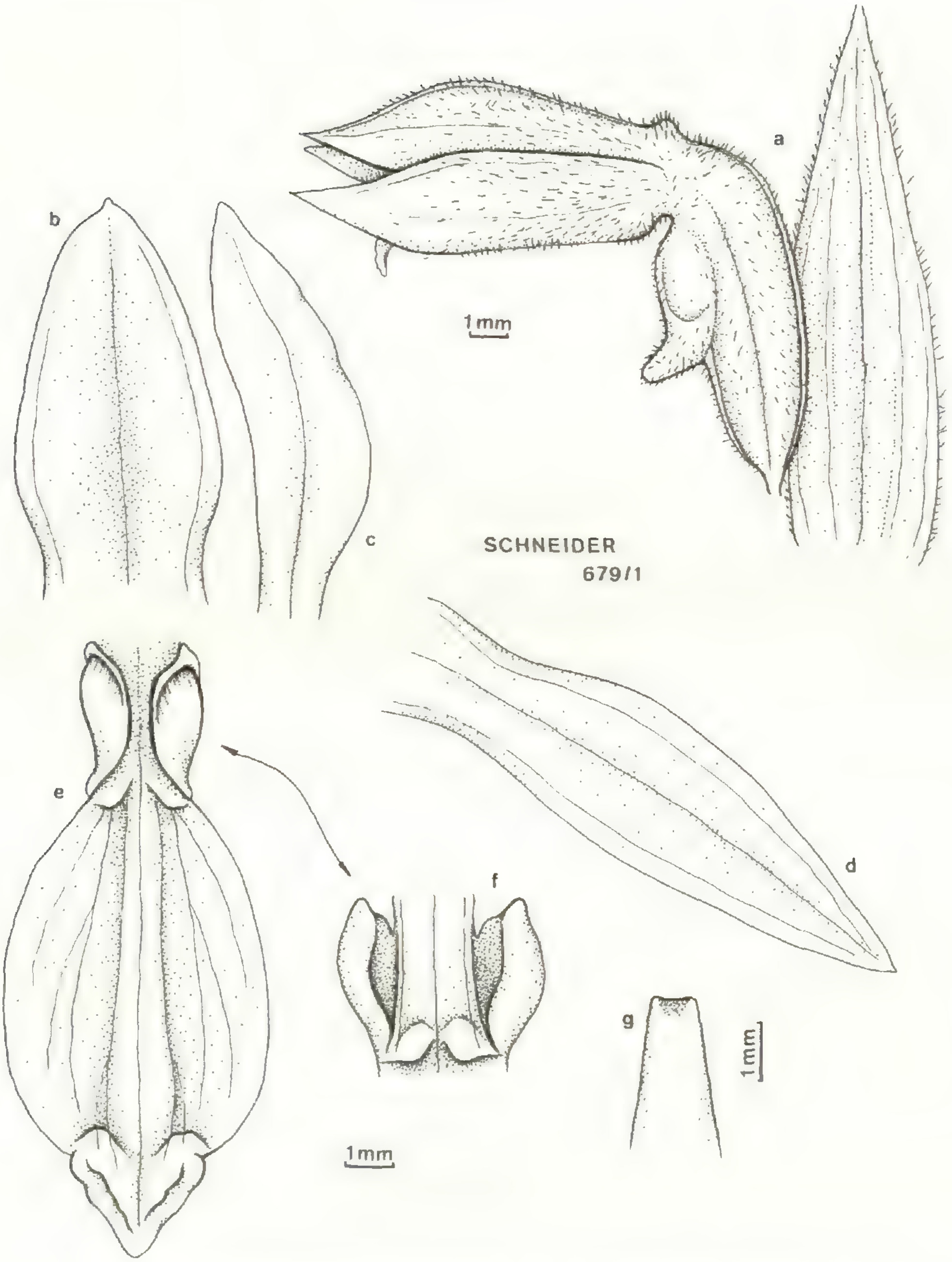


Figure 1. *Pelexia cundinamarcae* Szlach.: a—flower and floral bract; b—dorsal sepal; c—petal; d—free portion of lateral sepal; e—lip; f—basal lip auricles, spread; g—rostellum remnant.

lateral sepals 12.5 mm long, 3 mm wide, lanceolate, acute, slightly asymmetric, 3-nerved, glandular outside. Petals 11.5 mm long, 2.6 mm wide, linear-falcate, acute, single-nerved, slightly adnate to the dorsal sepal, ciliate on outer margins. Lip boat-formed, straight, shortly clawed; claw very thick in the center. Hypochile

12.5–13 mm long, 7.2 mm wide, obovate in general outline, thickened and papillate along midnerve and near the base, thin on margins: basal lip auricles 4–5 mm long, 4.7–5.5 mm wide when spread, connate with the claw with free apices about 1.3–1.5 mm long, fleshy, very thick. Epichile 3.5 mm long, 4–4.2 mm wide, obovate to cordate, obtuse to subacute, papillate, thicker than hypochile, fleshy. Gynostemium 9.5 mm long, erect; column foot adnate to the ovary on distance 6.5 mm long, with free apical part 2 mm long; rostellum 3 mm long, broad at base; viscidium 0.9 mm long; rostellum remnant 2.3 mm long; anther 3.6 mm long.

TYPE: COLOMBIA, Deptos. Cundinamarca-Boyaca—entre Villa Pinzon y Ventaquemada, 2800–2900 m. *Schneider 679/1,* 30 March 1953 (HOLOTYPE: COL 68326).

PARATYPE: COLOMBIA, Dept. Boyaca—bei Ventaquemada, 288–2900 m. *Schneider 679,* 30 March 1953 (s).

ETYMOLOGY: eipthet of this new entity based on the name of the Department in Colombia where the species was found.

*Pelexia cundinamarcae* is characterized by the position of the perianth versus ovary, shape of the spur and lip form, i.e., perianth segments set perpendicularly on the ovary apex; nectar spur is saccate with narrow, finger-like projection on apex; basal lip auricles are fleshy, thick, connate with thick claw and equal in length with the small, triangular and very fleshy epichile. Hypochile is obovate to cordate.

*Pelexia cundinamarcae* is a terrestrial plant, found in dense, moist forest. Sepals and petals are green, lip is greenish.

**PELEXIA ASINUS**, *sp. nov.* (Figure 2)

Pelexiae novofriburgensi affinis, sed floribus strictis, apice plus minusve patentibus, pedicello longo, erecto, calcari coniformi, apice soluto, auriculis labellis magnis, carnosis, epichilio transverse ovali duplo longioribus et hypochilio ovato-rhomboidali recedit.

Roots fleshy, clustered. Stem 520 mm tall, 6 mm in diameter at base, about 1 mm in diameter below inflorescence, erect, slightly pendulous in upper part, delicate, above the leaves sparsely glandular, densely glandular along inflorescence axis. Cauline bract single, narrow, acute, short, herbaceous, sparsely glandular at base.

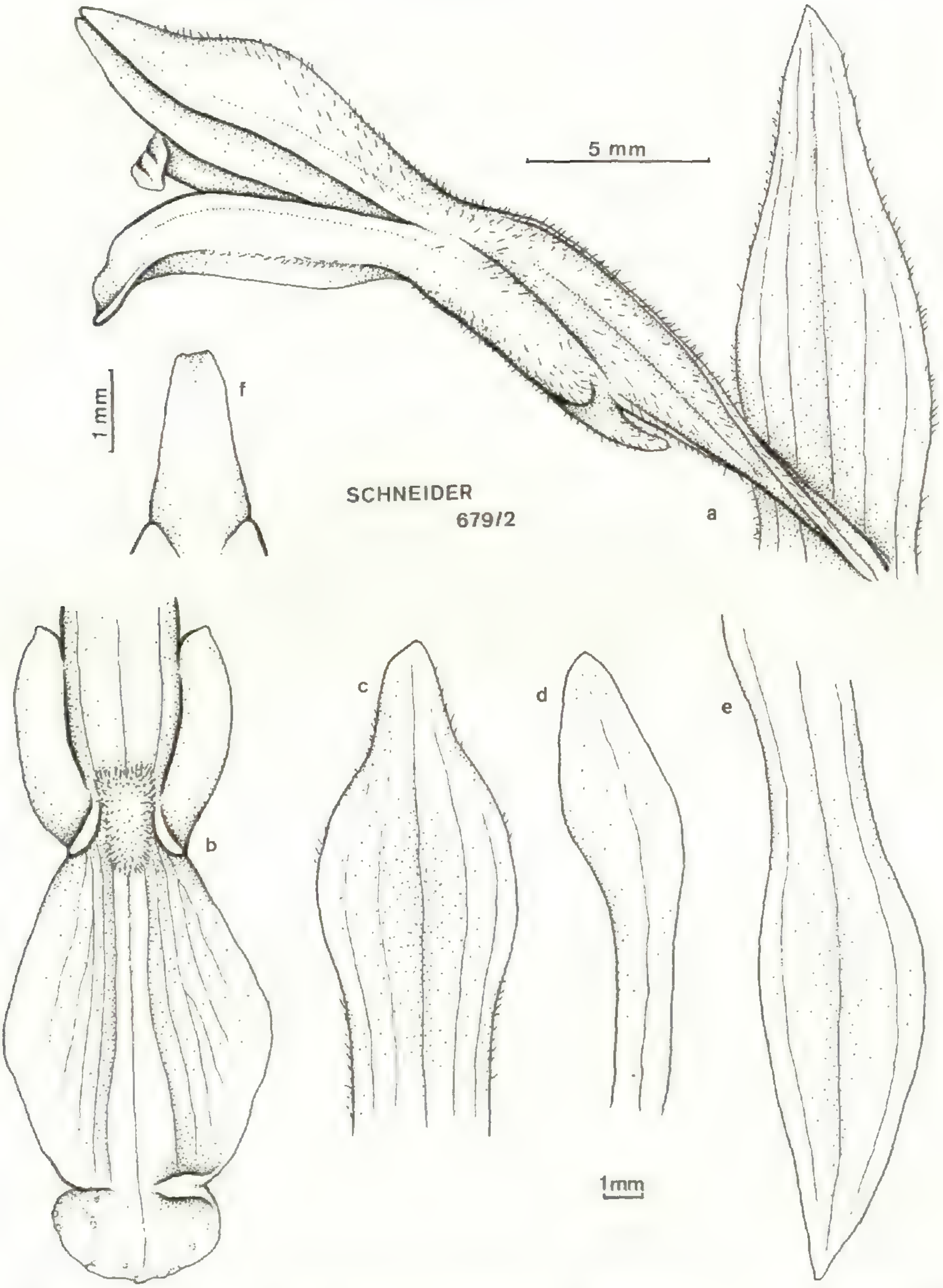


Figure 2. *Pelexia asinus* Szlach.: a—flower with floral bract; b—lip; c—dorsal sepal; d—petal; e—free portion of lateral sepal; f—rostellum remnant.

Leaves 5, forming a basal rosette and 2 on the stem; petiole 120 mm long, narrow, delicate; blade 85–100 mm long, 25–28 mm wide, lanceolate, acute, asymmetric, thin, delicate, reddish tinge. Inflorescence 120 mm long, 10-flowered, lax, subsecund. Flowers erect, medium-sized, with narrow slightly falcate spur. Floral bracts

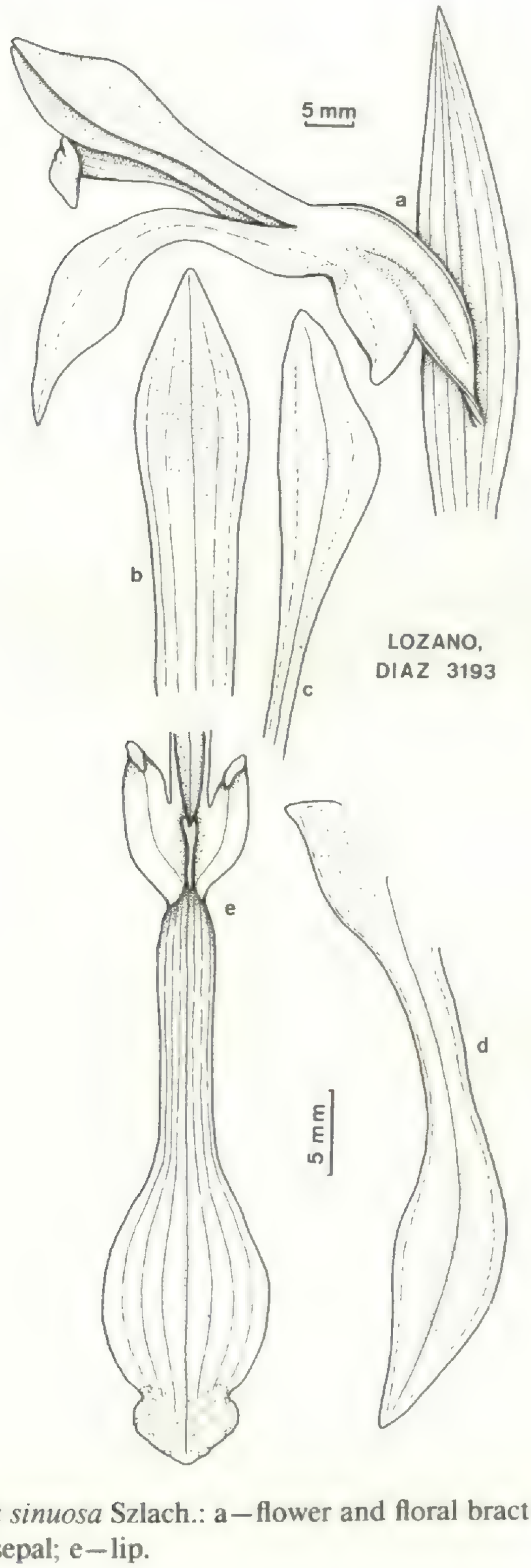


Figure 3. *Pelexia sinuosa* Szlach.: a—flower and floral bract; b—dorsal sepal; c—petal; d—lateral sepal; e—lip.

24 mm long, ovate-lanceolate, subacute, herbaceous, thin, glandular outside. Pedicel about 5–7 mm long, twisted. Ovary 16 mm long, narrow, densely glandular. Dorsal sepal 16.5 mm long, 5 mm wide, oblong, widest and concave in the middle, obtuse, rather fleshy, densely glandular outside in the basal half. Free part of lateral sepals 20 mm long, 4 mm wide, more or less erect, lanceolate, acute, fleshy, densely glandular outside in the basal half. Petals 16.5 mm long, 3.5 mm wide, falcate-oblanceolate, obtuse, single-nerved, glandular up to ¾ on outer margins. Lip straight with the apex bent forward, clawed; basal lip auricles 6 mm long, 1.6 mm wide, almost completely connate with the claw, free portion about 1 mm long, very thick, fleshy; hypochile 10 mm long, 8 mm wide, obovate, thickened along midnerve, margins thin, agglutinate to the clinandrium; epichile 3 mm long, 4.8 mm wide, elliptic, obtuse, fleshy, papillate. Gynostemium 12 mm long, erect; column foot adnate to the ovary along 7 mm, with free 2.5 mm apical part; rostellum remnant 2 mm long, broad at base; anther 4 mm long.

TYPE: COLOMBIA, Dept. Cundinamarca—Rio Sabaneta, mas abajo de El Dintel, 2200 m. *Schneider 679/2,* 13 June 1953 (HOLOTYPE: COL). ETYMOLOGY: *asinus* (Lat.)—donkey; an allusion to the general outline of the lip, which suggests the head of this animal.

At first glance *Pelexia asinus* seems to be similar to *P. novofriburgensis* (Reichenb. f.) Garay, but it is easy to distinguish by the erect flowers, set on the long and erect pedicel, narrow conical-falcate spur apex, very large and fleshy basal lip auricles, which are about twice the size of the elliptic epichile. Hypochile is obovate.

**PELEXIA SINUOSA**, *sp. nov.* (Figure 3)

Habitu Pelexiae funckianae similis, sed vaginis caulinis multis, floribus majoribus et inflorescentia densa differt. Bracteae longae, intus glandulosae. Labellum basi angulato-flexuosum, plico crasso, carnoso inter auriculis praeditum.

Roots fleshy, clustered. Stem 370 mm tall, 5–7 mm in diameter at base, 2–3 mm in diameter below inflorescence, erect, rather stout, glandular in upper half, completely covered by cauline bracts. Cauline bracts 6–12, longer than internodes, reach the inflores-

cence, lanceolate, spacious, acute, herbaceous, uppermost glandular at base. Leaves 7, forming a basal rosette; petiole 55–90 mm long, narrow; blade 45–90 mm long, 18–40 mm wide, broad-lanceolate, acute, seems to be fleshy. Inflorescence 130–180 mm long, 15–25-flowered, dense. Flowers very large, suberect, with saccate spur. Floral bracts 34–43 mm long, lanceolate to oblong-lanceolate, acute, thin, herbaceous, glandular outside. Pedicel 5 mm long, twisted. Ovary 18–23 mm long, narrow, almost erect, glandular. Dorsal sepal 28–30 mm long, 5.5–6.5 mm wide, oblong-lanceolate, subacute, thin, delicate, concave at apex, densely glandular outside. Lateral sepals 34–35 mm long, 4–4.5 mm wide, falcate-lanceolate, acute, thin, glandular outside. Petals 28–30 mm long, 4.8–5.5 mm wide, linear in lower part, falcate-lanceolate in upper, acute to obtuse, thin, glandular on outer margins. Lip set on long and narrow claw, basal lip auricles partially free from claw (2.3–2.8 mm long), 4.7–5 mm wide when spread, thickened at apices, ciliate outside; between auricles fleshy, papillate ridge, lip strongly S-incurved above the ridge; hypochile 28–30 mm long, 8.5–9.8 mm wide, thin, delicate, more or less linear in basal part and ovate in apical, sometimes with two small knobs at apex, fused with the column; epichile 4–5 mm long, 6–6.5 mm wide, cordate, obtuse, papillate, thicker than hypochile, bent forward in natural position. Gynostemium 21–25 mm long, slender, erect; column foot adnates to the ovary along 8.5–10 mm, with free apex 4 mm long; rostellum 3–4 mm long, membraneous, delicate; viscidium 1–1.5 mm long; rostellum remnant 3 mm long; anther 6 mm long; pollinarium 7.2–8 mm long.

TYPE: COLOMBIA, Dept. del Choco—kilometro 55 de la carretera Ansermanuevo-San Jose del Palmar, 1700–1950 m. Terrestre. Flores verdes, labelo verde amarilliento. *Lozano & Diaz 3193,* 19 March 1980 (HOLOTYPE: COL 200472).

PARATYPE: COLOMBIA, Dept. de Bolivar—requon du rio San Jorge. *Claes 32,* sine dat. (P).

ETYMOLOGY: *sinuosa* (Lat.)—sinous; in reference to the S-curvature of the lip base.

This new species is superficially similar to *P. funckiana* (A. Rich. & Gal.) Schlecht., but the flowers are almost twice as large as in the last species. They are arranged in multiflowered and dense inflorescence. Cauline bracts are numerous and longer than internodes covering the whole stem completely. Very long floral

bracts are glandular outside. But the most characteristic feature of *P. sinuosa* is S-formed lip bending in the anterior portion with fleshy, thick ridge between basal lip auricles.

## ACKNOWLEDGMENTS

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# ALGAL VEGETATION OF THE YORK RIVER ESTUARY AND THE ADJACENT OPEN COAST OF SOUTHERN MAINE[1]

ARTHUR C. MATHIESON, EDWARD J. HEHRE, AND MARTIN COSTA

## ABSTRACT

A total of 72 seaweed taxa were recorded from the York River Estuary, Maine, including 29 Rhodophyceae, 19 Phaeophyceae and 24 Chlorophyceae. A synopsis of several distributional patterns is given, as well as floristic comparisons of the York River with two nearby open coastal sites in Maine (Cape Neddick and Sea Point) and 12 estuarine locations within New Hampshire and northern Massachusetts. In contrast to the Great Bay Estuarine System (New Hampshire/Maine) where coastal species occur upstream to approximately 8.5 miles, a relatively rapid attrition of species occurs within the York River after 2–3 miles, presumably due to hydrographic variability, the dominance of saltmarsh habitats and reduced availability of rocky substrata. Overall, species composition within the York River compares favorably with several mid-estuarine environments within the Great Bay Estuary as well as saltmarsh habitats of the Hampton-Seabrook Estuary System (New Hampshire). Relatively few of the "southerly" taxa common to the Great Bay Estuary are present within the York River and Hampton-Seabrook Estuary, presumably because of a lack of suitable habitat. Three floristic records of particular interest include the presence of *Fucus vesiculosus* megecad *limicola* from the York River Estuary, and the occurrence of *Porphyra amplissima* and *Codium fragile* ssp. *tomentosoides* from southern Maine.

Key Words: seaweeds, estuarine, coastal, York River, Maine, New Hampshire, Massachusetts

## INTRODUCTION

In contrast to the southeastern United States, where saltmarsh (*Spartina* spp.) and eelgrass communities (*Zostera marina*) are dominant primary producers of organic carbon within estuarine habitats, seaweeds play a major role within north temperate estuaries of the Gulf of Maine (Josselyn and Mathieson, 1980). Estuarine seaweeds within the latter geography provide valuable habitats for a myriad of organisms, generate significant amounts of organic carbon via primary productivity, and contribute to detrital cycles and an "outwelling" of biological productivity to

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[1] Scientific Contribution Number 1830 from the New Hampshire Agricultural Experiment Station; also issued as Contribution Number 276 from the Jackson Estuarine Laboratory and the Center for Marine Biology.

nearshore coastal waters (Josselyn and Mathieson, 1978, 1980; Mann, 1972, 1982). Although these fundamental roles are becoming better known, very few detailed assessments of estuarine seaweed resources within the Gulf of Maine exist, except from New Hampshire (Mathieson and Fralick, 1972; Mathieson and Hehre, 1982, 1983, 1986; Mathieson and Penniman, 1986b, 1991; Mathieson et al., 1981) and Massachusetts (Mathieson and Fralick, 1973; Webber and Wilce, 1971). Thus, the only comprehensive seasonal collections of estuarine seaweeds in Maine have been made within the Piscataqua and Salmon Falls Rivers of the Great Bay Estuary System (cf. Mathieson and Hehre, 1986; Mathieson and Penniman, 1991), while only selected collections have been made at other northernmost sites (Bell and MacFarlane, 1933; Eaton, 1873; Stone et al., 1970).

The present study was initiated to enhance our knowledge of Maine estuarine seaweed populations. Specifically, we have summarized distributional and floristic patterns of seaweed populations within the York River Estuary (Maine), comparing them with previous synopses of the Hampton-Seabrook (New Hampshire), Merrimack River (Massachusetts) and Great Bay Estuarine Systems (New Hampshire and Maine), including the various subsets of the latter ecosystem (Figures 1 and 2). The proximity of the four estuarine systems within the southern Gulf of Maine (Figure 1), plus their varying sizes, habitats, industrial development and eutrophication, provides several meaningful comparisons.

## METHODS AND MATERIALS

Seasonal collections and observations were made at twenty sites within the York River Estuary, ranging from just outside York Harbor to a point about 1.5 miles below the river's tidal headwater (Figure 2, Table 1). A detailed description of each study site, including its location, habitat(s) and substrata is given in Appendix 1. Collections were made during 1978, 1985 and periodically thereafter. Overall, methods of collection and identification were similar to those outlined in Mathieson and Penniman (1991). Representative samples of all conspicuous seaweeds at each site were collected from the littoral (on foot) and sublittoral zones (by SCUBA). The nomenclature of South and Tittley (1986) was applied for most taxa. The author(s) of each binomial and many

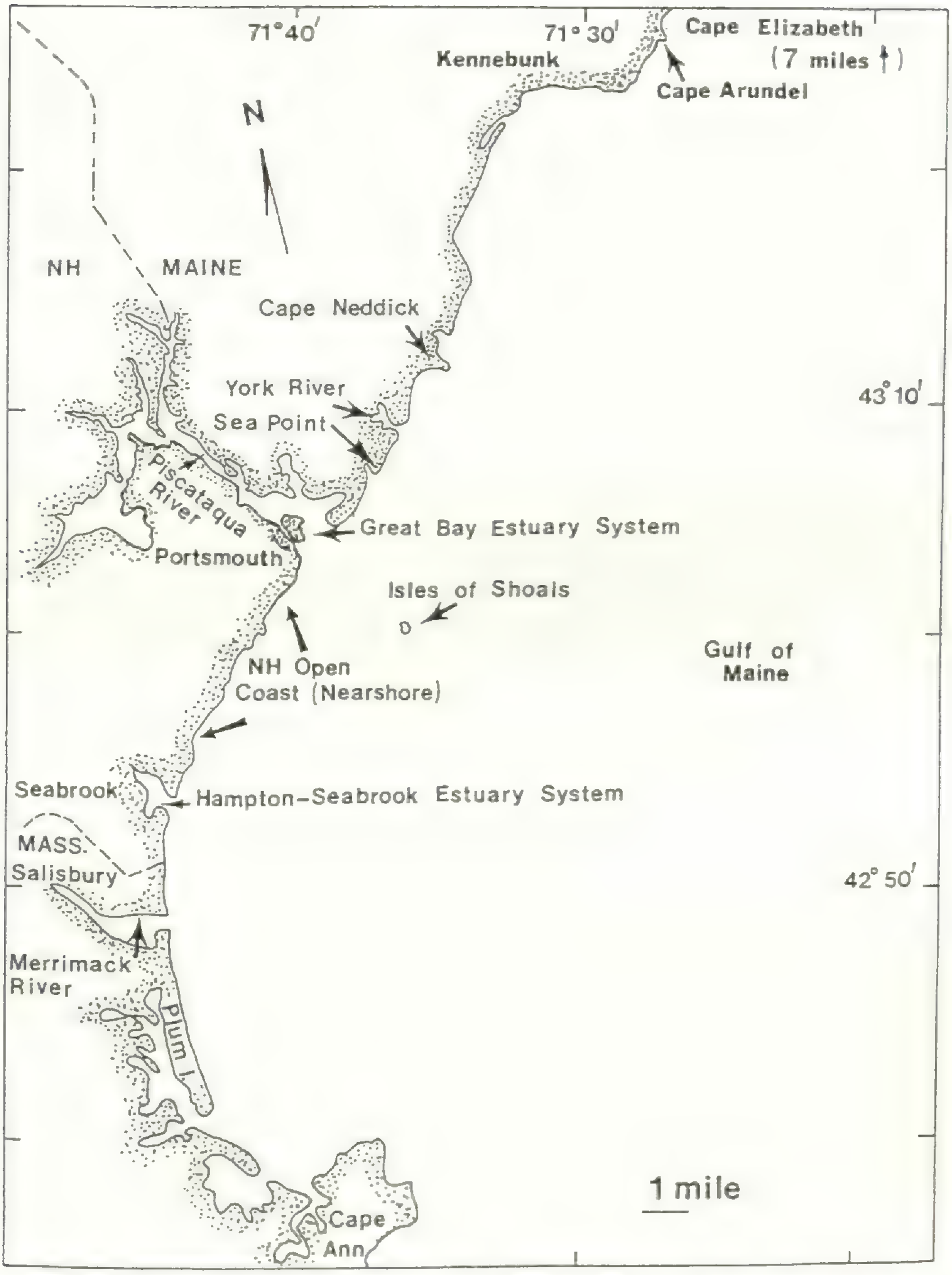
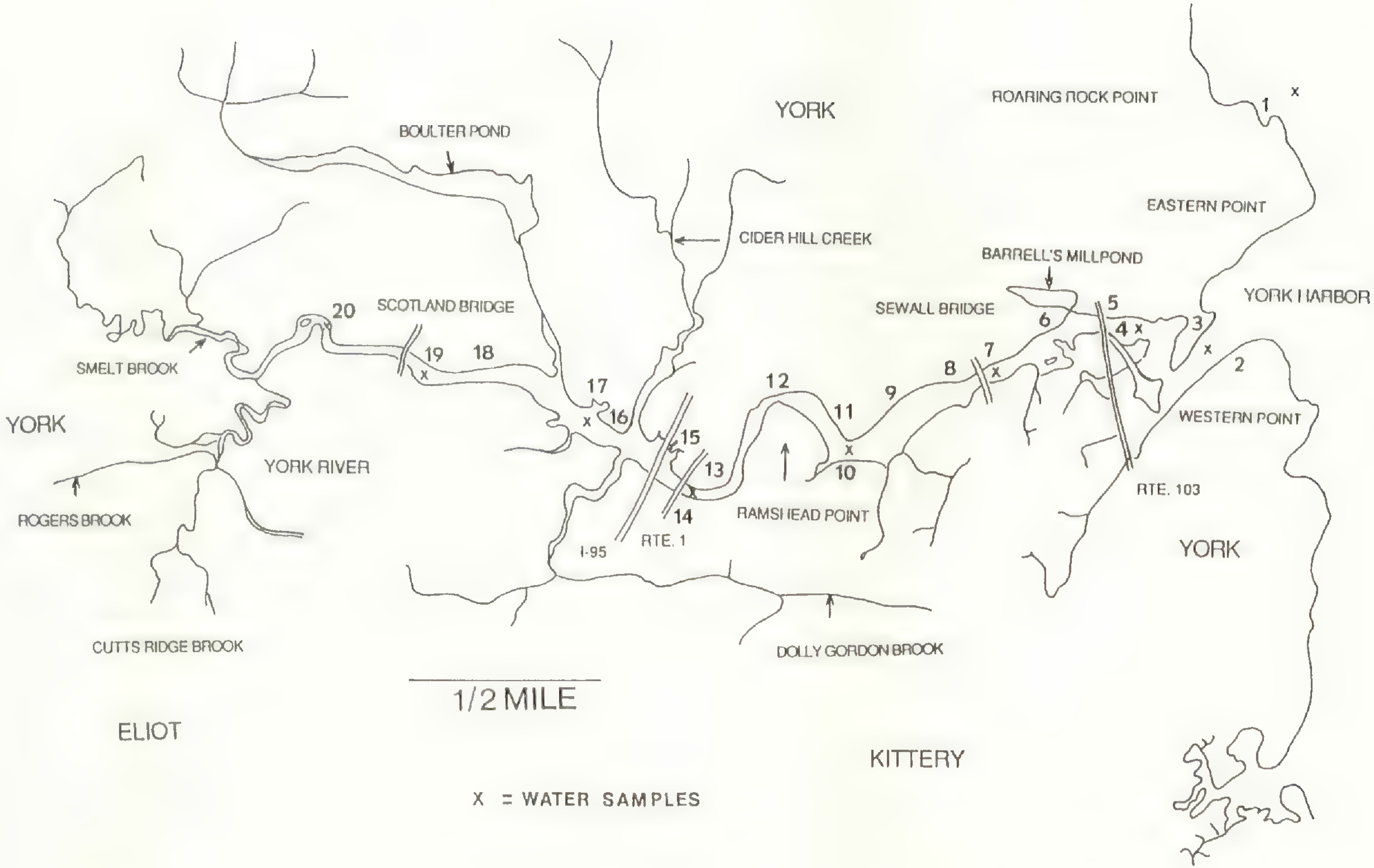



Figure 1. The northern New England coastline between southern Maine and northern Massachusetts showing the locations of the York River, Great Bay, Hampton-Seabrook and Merrimack River Estuaries, plus Cape Neddick and Sea Point, Maine.

pertinent nomenclatural changes since Taylor (1957) are included in Table 2. Approximately 500 voucher specimens are deposited in the Albion R. Hodgdon Herbarium (NHA) at the University of New Hampshire in order to document the river's flora. A com-


YORK
ROARING ROCK POINT
1
BOULTER POND
EASTERN POINT
CIDER HILL CREEK
BARRELL'S MILLPOND
SEWALL BRIDGE
YORK HARBOR
SCOTLAND BRIDGE
20
19
18
SMELT BROOK
17
16
12
11
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5
4
3
2
WESTERN POINT
YORK
YORK RIVER
15
13
10
RTE. 103
ROGERS BROOK
14
RAMSHEAD POINT
I-95
RTE. 1
YORK
CUTTS RIDGE BROOK
DOLLY GORDON BROOK
1/2 MILE
ELIOT
KITTERY
X = WATER SAMPLES

parison of two nearshore open coastal sites in southern Maine (Cape Neddick and Sea Point) plus twelve other estuarine habitats between Maine and Massachusetts is given (Figure 1, Table 1), utilizing several published records (Mathieson, 1979; Mathieson and Fralick, 1972, 1973; Mathieson and Hehre, 1986; Mathieson et al., 1981; Mathieson and Penniman, 1986b, 1991).

Surface water temperature, salinity, pH and total suspended solids were recorded (winter/spring, 1978) at eight sites, ranging from the mouth to the tidal headwaters. Temperature and salinity were recorded (*in situ*) with a hand-held thermometer and refractometer (.1°C & .5‰ accuracy), while pH was measured with an Orian pH meter. Total suspended solids (mg/liter) were determined according to Strickland and Parsons (1968). Seasonal assessments (approx. monthly) of the same parameters were documented near the mouth of York Harbor between September, 1991 and January, 1992 (i.e., near station 4 in Appendix 1) in conjunction with a comparative investigation of the York and Piscataqua Rivers (R. Langan, unpubl. data). Records of *in situ* temperature and salinity were recorded with a YSI conductivity meter (model CST), while ionic concentrations were measured with a Fisher Alumet pH meter. Total suspended solids were determined as outlined above.

## HABITAT DESCRIPTION

The York River Estuary, located in southern York County, Maine, between Cape Neddick (York) and Sea Point (Kittery), extends approximately 7 miles inland from its mouth near Western Point to its tidal headwaters in East Eliot (Figures 1 and 2). Most of the estuary is within York, except for a small tidal marsh in East Eliot. The source of the river is York Pond, which is in the northeast corner of Eliot township. Three major brooks drain into the river near its headwaters (Smelt Brook in York and Cutts Ridge and Rogers Brooks in Eliot), while three large tributaries (Boulter Pond Brook, Cider Hill Creek and Dolly Gordon Brook) are within .5 mile of the Maine Turnpike (I-95). Boulter and

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Figure 2. Twenty study sites within the York River Estuary (Maine) and the adjacent open coast, including the location of water sampling sites.

Table 1. Synopsis of collecting sites between southern Maine and northern Massachusetts, including the York River Estuary.

| Geographical Areas | Individual Sites | Distance from Open Coast (miles) | References |
|---|---|---|---|
| Nearshore open coastline of southern Maine: Cape Neddick (York) and Sea Point (Kittery) | 2 | = nearshore open coast | Mathieson (1979)<br>Mathieson & Hehre (1986) |
| York River Estuary, Maine (York and Eliot) | 20 | 0–7 | present study |
| Great Bay Estuary System New Hampshire–Maine | 147 | 0–22.7 | Doty and Newhouse (1954)<br>Hehre and Mathieson (1970)<br>Mathieson and Hehre (1986)<br>Mathieson et al. (1981, 1983)<br>Mathieson and Penniman (1986b, 1991)<br>Norall et al. (1982)<br>Reynolds and Mathieson (1975) |
| Piscataqua River, N.H./Maine | 59 | 0–12.1 | Mathieson and Hehre (1986)<br>Mathieson et al. (1977) |
| Little Bay, New Hampshire | 21 | 8.6–12.4 | Reynolds and Mathieson (1975) |
| Great Bay, New Hampshire | 16 | 12.9–15.7 | Mathieson and Hehre (1986)<br>Mathieson et al. (1982) |
| Bellamy River, New Hampshire | 10 | 10.4–14.3 | Mathieson and Hehre (1986) |
| Cocheco River, New Hampshire | 17 | 12.6–15.8 | Mathieson and Hehre (1986) |
| Lamprey River, New Hampshire | 9 | 15.8–17.5 | Mathieson and Hehre (1986) |
| Oyster River, New Hampshire | 14 | 11.5–14.2 | Mathieson and Hehre (1986) |
| Salmon Falls River, Hew Hampshire/Maine | 16 | 12.5–16.5 | Mathieson and Hehre (1986) |
| Sqamscott River, New Hampshire | 16 | 16.2–22.7 | Mathieson and Hehre (1986) |
| Winnicut River, New Hampshire | 4 | 15.8–17.3 | Mathieson and Hehre (1986) |
| Hampton–Sea- | 49 | 0–5.2 | Hehre and Mathieson (1970) |

Table 1. Continued.

| Geographical Areas | Individual Sites | Distance from Open Coast (miles) | References |
|---|---|---|---|
| brook Estuary, New Hampshire | | | Mathieson and Fralick (1972)<br>Mathieson and Hehre (1986) |
| Merrimack River Estuary, Massachusetts | | | Mathieson and Fralick (1973) |

Middle Ponds, which lie to the north, are sources of the first two tributaries, while Dolly Gordon Brook originates from a saltmarsh to the southeast.

As outlined in Appendix 1, the substratum available for seaweed growth is both limited and scattered. Boulders, cobbles, pebbles and rock outcrops primarily occur in high energy areas (i.e., due to waves) near the mouth of the river, while York Harbor is mostly sandy (cf. Figure 2). Several artificial structures (bridge abutments, pilings and boat moorings) are located immediately upstream from York Harbor, while saltmarshes dominate most shorelines between Route 1A (Sewall Bridge) and tidal headwaters (Figure 2). The main channel of the river is relatively straight, with only one large meander at Ramshead Point, as opposed to its tributaries that have sharply developed meanders indicative of youthful streams. About one mile upstream from Scotland Bridge the river branches into two major channels associated with the confluence of Smelt Brook and the York River (Figure 2). A major oxbow occurs downstream from this confluence, while several smaller ones are found upstream. Each inner channel has a steep-sided shoreline that cuts across broad expanses of saltmarsh with peat and clay soils. The saltmarshes are dominated by *Spartina alterniflora, S. patens* and *Juncus gerardii,* along with several other vascular plants. In some instances (e.g., near house construction), the marshes are very narrow and only contain *S. alterniflora.* Overall, the most expansive mudflat habitats are found near York Harbor where saltmarshes are either reduced or absent.

Figure 3 illustrates "typical" winter/spring hydrographic conditions within the estuary. Surface water temperatures ranged from approximately 3.0°C (0 miles) to 0°C (4.4 miles), while salinities were approximately 31‰ on the open coast and varied from 0–16‰ at station 8 (4.4 miles inland). Thus, surface water temperatures during late winter and spring are relatively low and

Table 2. Systematic list of algal species found within the York River Estuary and the adjacent open coast of Maine, with synonyms in parentheses referring to names in Taylor (1957).

CHLOROPHYCEAE

MICROSPORALES

**Microsporaceae**

*Microspora pachyderma* (Wille) Lagerheim

ULOTRICHALES

**Ulotrichaceae**

*Ulothrix flacca* (Dillwyn) Thuret in Le Jolis

*Ulothrix speciosa* (Carmichael ex Harvey in Hooker) Kützing

ULVALES

**Percursariaceae**

*Percursaria percursa* (C. Agardh) Bory

**Ulvaceae**

*Capsosiphon fulvescens* (C. Agardh) Setchell et Gardner

*Enteromorpha clathrata* (Roth) Greville

*Enteromorpha flexuosa* (Wulfen ex Roth) J. Agardh ssp. *paradoxa* (Dillwyn) Bliding

*Enteromorpha intestinalis* (Linnaeus) Link

*Enteromorpha linza* (Linnaeus) J. Agardh

*Enteromorpha prolifera* (O. F. Müller) J. Agardh

*Ulva lactuca* Linnaeus

*Ulvaria obscura* (Kützing) Gayral [= *Monostroma fuscum* (Postels et Ruprecht) Wittrock]

*Ulvaria oxysperma* (Kützing) Bliding [= *Monostroma oxyspermum* Kützing]

**Monostromataceae**

*Blidingia minima* (Nägeli ex Kützing) Kylin [includes *Enteromorpha minima, E. micrococca, E. marginata*]

*Monostroma grevillei* (Thuret) Wittrock

*Monostroma pulchrum* Farlow

PRASIOLALES

**Prasiolaceae**

*Prasiola stipitata* Suhr in Jessen

ACROSIPHONIALES

**Acrosiphoniaceae**

"*Codiolum pusillum*" (Lyngbye) Kjellman [= sporophytic stage in the life history of *Urospora wormskioldii* and probably conspecific with *Codiolum gregarium*]

*Urospora penicilliformis* (Roth) Areschoug

*Urospora wormskioldii* (Mertens in Hornemann) Rosenvinge [includes *U. collabens* (C. Agardh) Holmes et Batters]

*Spongomorpha arcta* (Dillwyn) Kützing

*Spongomorpha spinescens* Kützing

Table 2. Continued.

CLADOPHORALES

**Cladophoraceae**

*Chaetomorpha brachygona* Harvey [including *C. cannabina* (Areschoug) Kjellman]
*Chaetomorpha linum* (O. F. Müller) Kützing
*Chaetomorpha melagonium* (Weber et Mohr) Kützing
*Chaetomorpha picquotiana* Montagne ex Kützing [= *C. atrovirens* Taylor]
*Cladophora sericea* (Hudson) Kützing [includes *C. glaucescens, C. rudolphiana, C. flexuosa* and *C. gracilis*]
*Rhizoclonium riparium* (Roth) Kützing ex Harvey
*Rhizoclonium tortuosum* (Dillwyn) Kützing

BRYOPSIDALES

**Bryopsidaceae**

*Bryopsis plumosa* (Hudson) C. Agardh

**Codiaceae**

*Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (van Goor) Silva

PHAEOPHYCEAE

ECTOCARPALES

**Ectocarpaceae**

*Ectocarpus fasciculatus* Harvey
*Ectocarpus siliculosus* (Dillwyn) Lyngbye [includes *E. dasycarpus, E. confervoides* and *E. penicillatus*]
*Giffordia granulosa* (J. E. Smith) Hamel
*Laminariocolax tomentosoides* (Farlow) Kylin [= *Ectocarpus tomentosoides* Farlow]
*Mikrosyphar porphyrae* Kuckuck
*Pilayella littoralis* (Linnaeus) Kjellman
*Spongonema tomentosum* (Hudson) Kützing [= *Ectocarpus tomentosus* (Hudson) Lyngbye]

**Ralfsiaceae**

*Petroderma maculiforme* (Wollny) Kuckuck
*Pseudolithoderma extensum* (P. Crouan et H. Crouan) S. Lund [= *Lithoderma extensum* (Crouan) Hamel]
*Ralfsia verrucosa* (Areschoug) J. Agardh
*Sorapion kjellmanii* (Wille) Rosenvinge

**Myrionemataceae**

*Ascocyclus distromaticus* Taylor

**Elachistaceae**

*Elachista fucicola* (Velley) Areschoug [includes *Elachista lubrica* Ruprecht]

CHORDARIALES

**Leathesiaceae (= Corynophlaeaceae)**

*Leathesia difformis* (Linnaeus) Areschoug

Table 2. Continued.

**Chordariaceae**
*Chordaria flagelliformis* (O. F. Müller) C. Agardh
*Eudesme virescens* (Carmichael ex Harvey *in* Hooker) J. Agardh

SPHACELARIALES

**Sphacelariaceae**
*Sphacelaria arctica* Harvey [= *Sphacelaria racemosa* Greville var. *arctica* (Harvey) Reinke]
*Sphacelaria cirrosa* (Roth) C. Agardh

DESMARESTIALES

**Desmarestiaceae**
*Desmarestia aculeata* (Linnaeus) Lamouroux
*Desmarestia viridis* (O. F. Müller) Lamouroux

DICTYOSIPHONALES

**Punctariaceae**
*Punctaria plantaginea* (Roth) Greville

**Dictyosiphonaceae**
*Dictyosiphon foeniculaceus* (Hudson) Greville

**Scytosiphonaceae**
*Petalonia fascia* (O. F. Müller) Kuntze
"*Ralfsia bornetii*" Kuckuck [sporophytic stage in the life history of *Petalonia fascia*]
*Scytosiphon lomentaria* (Lyngbye) Link var. *lomentaria*

LAMINARIALES

**Chordaceae**
*Chorda filum* (Linnaeus) Stackhouse
*Chorda tomentosa* Lyngbye

**Laminariaceae**
*Agarum cribrosum* (Mertens) Bory
*Laminaria digitata* (Hudson) Lamouroux
*Laminaria saccharina* (Linnaeus) Lamouroux
*Saccorhiza dermatodea* (de la Pylaie) J. Agardh

**Alariaceae**
*Alaria esculenta* (Linnaeus) Greville

FUCALES

**Fucaceae**
*Ascophyllum nodosum* (Linnaeus) Le Jolis
*Ascophyllum nodosum* ecad *scorpioides* (Reinke) Hauck [= *Ascophyllum mackaii* (Turner) Holmes et Batters]
*Fucus distichus* Linnaeus emend. Powell ssp. *distichus* Powell [= *Fucus filiformis* Gmelin]
*Fucus distichus* Linnaeus emend. Powell ssp. *edentatus* (de al Pylaie) Powell [= *Fucus edentatus* de la Pylaie]

Table 2. Continued.

*Fucus distichus* Linnaeus emend. Powell ssp. *evanescens* (C. Agardh) Powell [= *Fucus evanescens* C. Agardh]
*Fucus spiralis* Linnaeus
*Fucus vesiculosus* Linnaeus

RHODOPHYCEAE: BANGIOPHYCIDAE

PORPHYRIDIALES

**Goniotrichaceae**
*Stylonema alsidii* (Zanardini) Drew [= *Goniotrichum alsidii* (Zanardini) Howe]

BANGIALES

**Erythropeltidaceae**
*Erythrotrichia carnea* (Dillwyn) C. Agardh

**Bangiaceae**
*Bangia atropurpurea* (Roth) C. Agardh
*Porphyra amplissima* (Kjellman) Setchell et Hus *in* Hus
*Porphyra linearis* Greville
*Porphyra miniata* (C. Agardh) C. Agardh
*Porphyra umbilicalis* (Linnaeus) J. Agardh

RHODOPHYCEAE: FLORIDEOPHYCIDAE

NEMALIALES

**Acrochaetiaceae**
*Audouinella alariae* (H. Jónsson) Woelkerling [= *Kylinia alariae* (H. Jónsson) Kylin]
*Audouinella purpurea* (Lightfoot) Woelkerling [= *Rhodochorton purpureum* (Lightfoot) Rosenvinge]
*Audouinella secundata* (Lyngbye) Dixon [includes *Kylinia secundata* and *K. virgatula*]

**Bonnemaisoniaceae**
*Bonnemaisonia hamifera* Hariot [= *Asparagopsis hamifera* (Hariot) Okamura]

PALMARIALES

**Palmariaceae**
*Devaleraea ramentacea* (Linnaeus) Guiry [= *Halosaccion ramentaceum* (Linnaeus) J. Agardh]
*Palmaria palmata* (Linnaeus) Kuntze [= *Rhodymenia palmata* (Linnaeus) Greville]

CRYPTONEMIALES

**Dumontiaceae**
*Dumontia contorta* (Gmelin) Ruprecht [= *D. incrassata* (O. F. Müller) Lamouroux]

**Choreocolacaceae**
*Harveyella mirabilis* (Reinsch) Schmitz et Reinke

Table 2. Continued.

**Kallymeniaceae**

*Callocolax neglectus* Schmitz ex Batters

*Callophyllis cristata* (C. Agardh) Kützing [= *Euthora cristata* (Linnaeus ex Turner) J. Agardh]

**Gloiosiphoniaceae**

*Gloiosiphonia capillaris* (Hudson) Carmichael ex Berkeley

HILDENBRANDIALES

**Hildenbrandiaceae**

*Hildenbrandia rubra* (Sommerfelt) Meneghini [= *H. prototypus* Nardo]

CORALLINALES

**Corallinaceae**

*Clathromorphum circumscriptum* (Strömfelt) Foslie [= *Phymatolithon evanescens* (Foslie) Foslie]

*Corallina officinalis* Linnaeus

*Dermatolithon pustulatum* (Lamouroux) Foslie [= *Lithophyllum pustulatum* (Lamouroux) Foslie]

*Leptophytum laeve* (Strömfelt) Adey [= *Lithothamnium laeve* (Strömfelt) Foslie]

*Lithophyllum corallinae* (Crouan frat.) Heydrich

*Lithothamnion glaciale* Kjellman

*Phymatolithon laevigatum* (Foslie) Foslie

*Phymatolithon lenormandii* (Areschoug in J. Agardh) Adey [= *Lithothamnion lenormandii* (Areschoug) Foslie]

*Pneophyllum fragile* Kützing [= *Fosliella lejolisii* (Rosanoff) Howe]

GIGARTINALES

**Phyllophoraceae**

*Ahnfeltia plicata* (Hudson) Fries

*Ceratocolax hartzii* Rosenvinge

*Gymnogongrus crenulatus* (Turner) J. Agardh [= *G. norvegicus* (Gunnerus) J. Agardh]

*Phyllophora pseudoceranoides* (Gmelin) Newroth et A. Taylor [= *P. membranifolia* (Goodenough et Woodward) J. Agardh]

*Phyllophora truncata* (Pallas) Zinova [includes *P. brodiaei* and *P. interrupta*]

**Petrocelidaceae**

*Mastrocarpus stellatus* (Stackhouse in Withering) Guiry [= *Gigartina stellata* (Stackhouse) Batters]

**Gigartinaceae**

*Chondrus crispus* Stackhouse

**Polyideaceae**

*Polyides rotundus* (Hudson) Greville [= *P. caprinus* (Gunnerus) Papenfuss]

Table 2. Continued.

**Cystocloniaceae**
*Cystoclonium purpureum* (Hudson) Batters
*Fimbrifolium dichotomum* (Lepeschkin) Hansen [= *Rhodophyllis dichotoma* (Lepeschkin) Gobi]

RHODYMENIALES

**Champiaceae**
*Lomentaria baileyana* (Harvey) Farlow
*Lomentaria clavellosa* (Turner) Gaillon
*Lomentaria orcadensis* (Harvey) Collins ex Taylor

CERAMIALES

**Ceramiaceae**
*Antithamnionella floccosa* (O. F. Müller) Whittick [= *Antithamnion floccosum* (O. F. Müller) Kleen]
*Callithamnion byssoides* Arnott ex Harvey in Hooker
*Callithamnion tetragonum* (Withering) S. F. Gray [= *C. baileyi* Harvey]
*Ceramium rubrum* (Hudson) C. Agardh
*Ceramium strictum* Harvey
*Plumaria plumosa* (Hudson) Kuntze [= *P. elegans* (Bonnemaison) Schmitz]
*Ptilota serrata* Kützing
*Scagelia pylaisei* (Montagne) Wynne [= *Antithamnion pylaisaei* (Montagne) Kjellman]

**Delesseriaceae**
*Membranoptera alata* (Hudson) Stackhouse [includes *M. denticulata* (Montagne) Kylin]
*Phycodrys rubens* (Linnaeus) Batters

**Dasyaceae**
*Dasya baillouviana* (Gmelin) Montagne [= *D. pedicellata* (C. Agardh) C. Agardh]

**Rhodomelaceae**
*Polysiphonia denudata* (Dillwyn) Greville ex Harvey
*Polysiphonia flexicaulis* (Harvey) Collins
*Polysiphonia harveyi* Bailey
*Polysiphonia lanosa* (Linnaeus) Tandy
*Polysiphonia nigra* (Hudson) Batters
*Polysiphonia nigrescens* (Hudson) Greville
*Polysiphonia subtilissima* Montagne
*Polysiphonia urceolata* (Lightfoot ex Dillwyn) Greville
*Rhodomela confervoides* (Hudson) Silva

uniform, while a conspicuous reduction in salinities occurs within inner estuarine habitats (3.3–4.4 miles), particularly during spring runoff (late March–April). The pattern of total suspended solids showed peak values near the open coast (approx. 177 mg/liter)

and a general decrease upstream (47–25 m/liter), except for a slight peak near the I-95 bridge (57 mg/liter); pH varied from approximately 8.2–8.0 between 0–2.4 miles, with lower values occurring upstream (7.7–7.4).

Seasonal variability of hydrographic conditions near York Harbor are illustrated in Figure 4. Surface water temperatures ranged from approximately 16.0°C (September, 1991) to 2.0°C (February), while salinities varied from approximately 32.0‰ (September, 1991) to 21.0‰ (April), pH from 8.4 (November, 1991) to 7.6 (December, 1992), and total suspended solids from 22.9 (February) to 5.6 mg/liter (December, 1992). Each parameter shows a relatively broad range throughout the year, with spring runoff occurring in late March–April. Greater hydrographic amplitudes were no doubt evident within inner estuarine stations (cf. Figure 3), although they weren't documented. Monthly values for total suspended solids during 1991–1992 were never as high as those recorded after a major "northeaster" during February of 1978 (approx. 177 mg/liter; Figure 3).

Overall, water quality within the York River appears to be very good, as the region is sparsely populated (particularly upriver of Route 1) and totally devoid of industry. The only signs of pollution are evident near Rice's Bridge (i.e., stations 13 and 14) where two discharge pipes occur. A localized enhancement of siltation and turbidity was evident during repair work on the I-95 Bridge (Figure 3).

## SPECIES COMPOSITION AND DISTRIBUTIONAL PATTERNS

A total of 131 taxa were recorded from the York River Estuary and two nearby open coastal sites in southern Maine (Cape Neddick and Sea Point), including 61 Rhodophyceae, 39 Phaeophyceae and 31 Chlorophyceae (Figure 5, Table 3). Seventy-two taxa were found in the York River (29 Rhodophyceae, 19 Phaeophyceae and 24 Chlorophyceae), while 59 were restricted to the open coast. The seaweeds within this open coastal-estuarine gradient exhibited three major distributional patterns (Figure 5, Table 3):

(1) Coastal—restricted to the nearshore open coast (59 taxa or 45%).
(2) Cosmopolitan—present in both estuarine and open coastal environments (45 taxa or 34%).

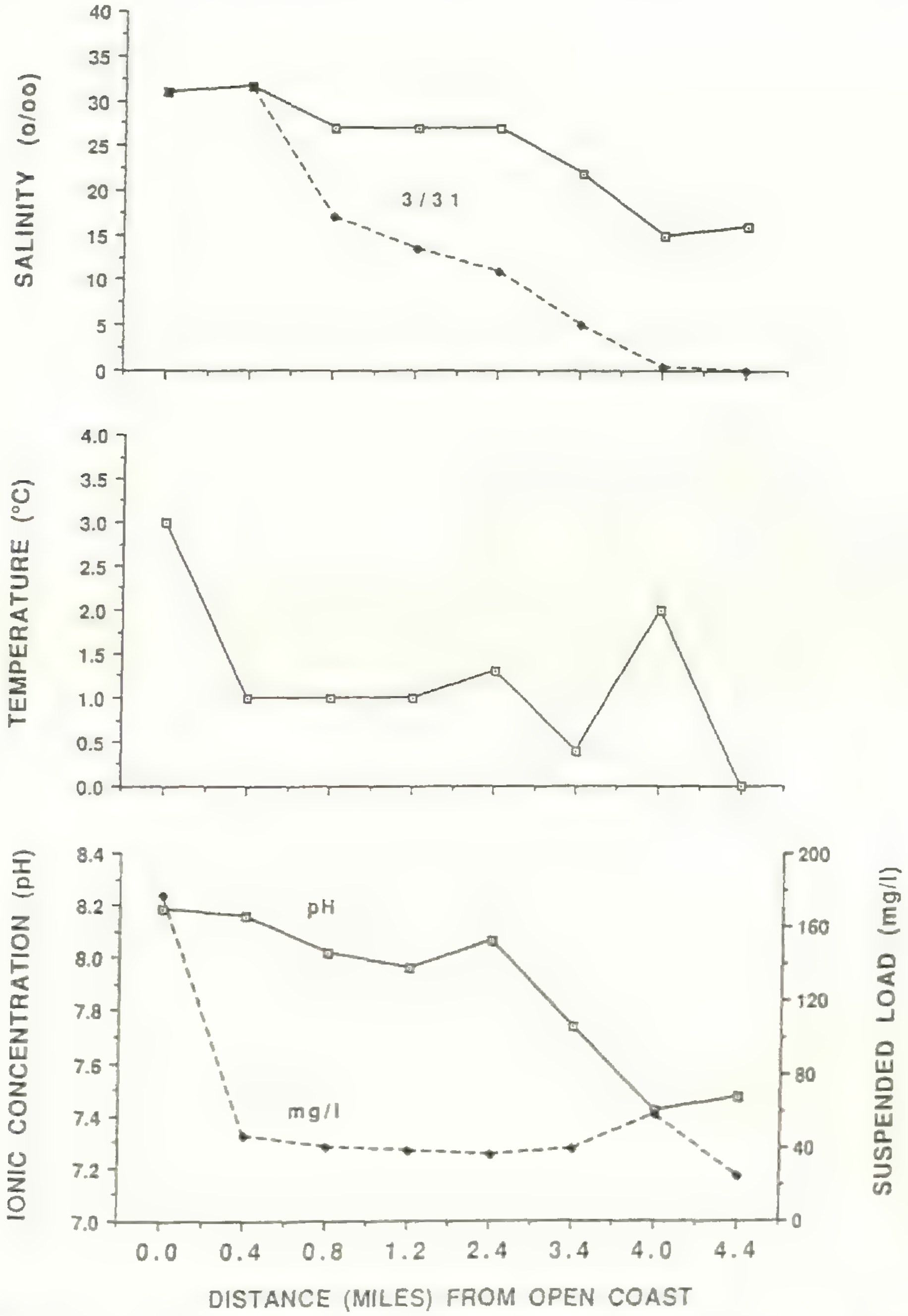


Figure 3. Surface water hydrographic conditions (i.e., temperature, salinity, pH and total suspended loads) within the York River Estuary during February and March (salinity only) of 1978.

(3) Estuarine—restricted to the York River Estuary (27 taxa or 21%).

As outlined in Table 3 approximately 47% of the coastal taxa occurred at both Cape Neddick and Sea Point, while the remain-

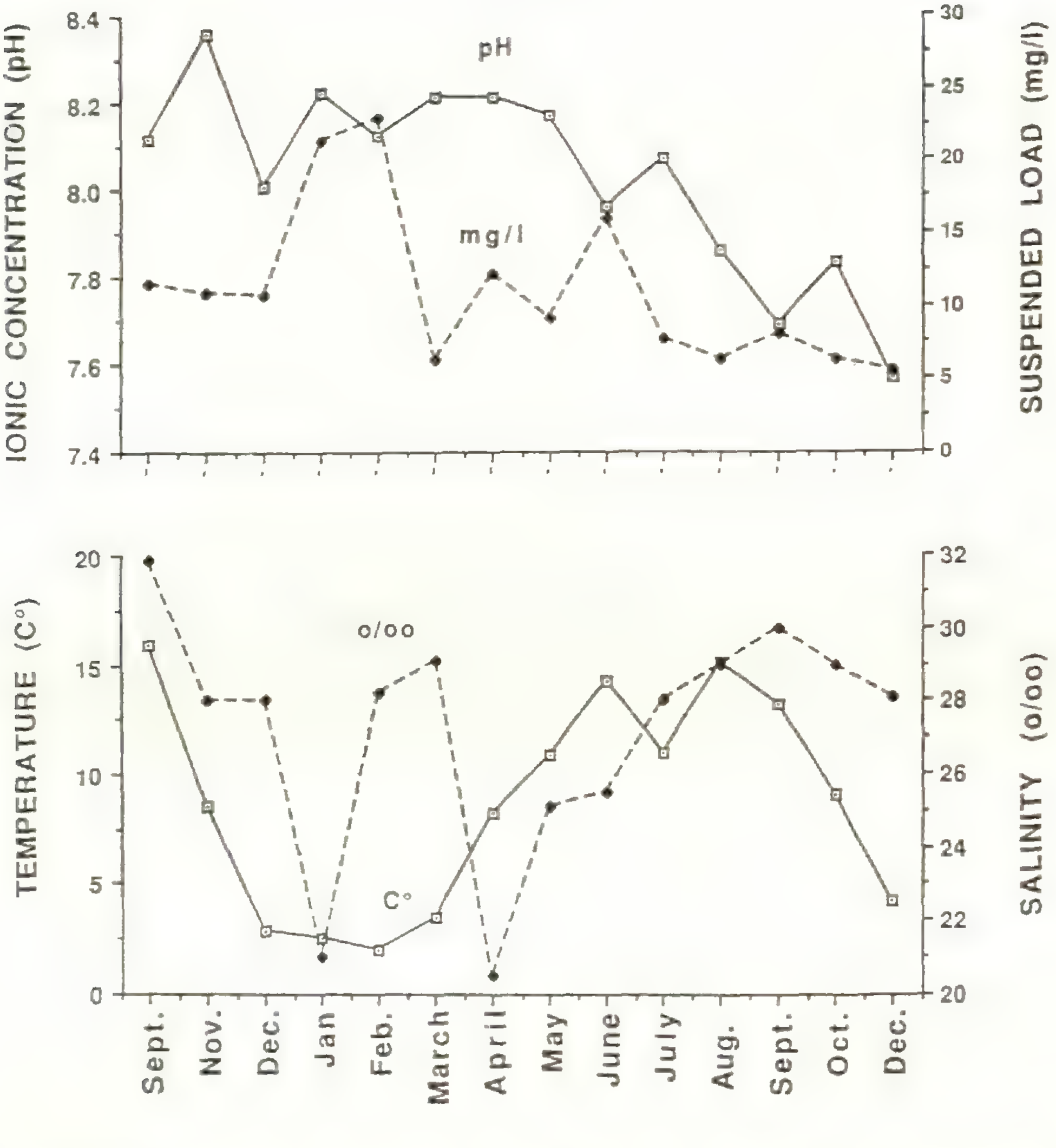


Figure 4. Monthly variability of surface water hydrographic conditions (i.e., temperature, salinity, pH and total suspended solids) at the mouth of the York River Estuary between September, 1991–December, 1992.

der (53%) were restricted to a single station (i.e., *Codiolum pusillum, Codium fragile* ssp. *tomentosoides, Enteromorpha linza, Prasiola stipitata, Ascocyclus distromaticus, Chorda filum, C. tomentosa, Dictyosiphon foeniculaceus, Eudesme virescens, Laminariocolax tomentosoides, Leathesia difformis, Mikrosyphar porphyrae, Punctaria plantaginea, Saccorhiza dermatodea, Sphacelaria arctica, S. cirrosa, Spongonema tomentosum, Antithamnionella floccosa, Audouinella alariae, A. purpurea, Callithamnion tetragonum, Devaleraea ramentacea, Gloiosiphonia capillaris, Gymnogongrus crenulatus, Harveyella mirabilis, Lomentaria or-*

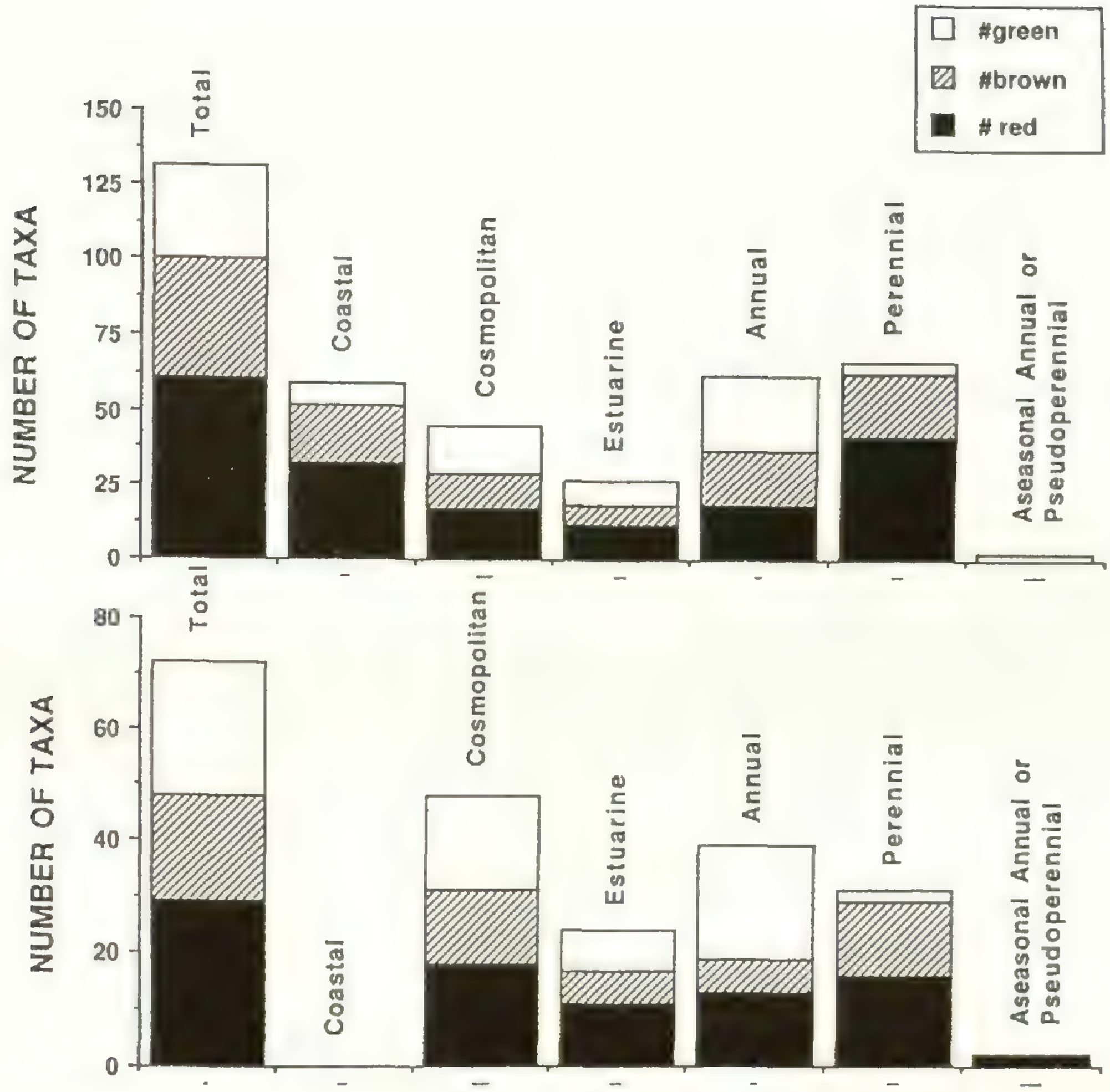


Figure 5. Patterns of species richness, local distribution and longevity of seaweed taxa within the York River Estuary and at two nearshore open coastal sites in southern Maine (Cape Neddick and Sea Point).

*cadensis, Plumaria plumosa, Pneophyllum fragile, Porphyra amplissima, P. linearis* and *Scagelia pylaisei*).

Cosmopolitan taxa exhibited varying estuarine distributional patterns (cf. Table 3). The fucoid brown algae *Ascophyllum nodosum* and *Fucus vesiculosus* plus the red alga *Dumontia contorta* occurred at 86–96% of coastal and estuarine stations, while twelve others occurred at >60% of these sites (e.g., *Blidingia minima, Enteromorpha intestinalis, Monostroma grevillei, Urospora penicilliformis, Ascophyllum nodosum* ecad *scorpioides, Petalonia fascia, Pilayella littoralis, Scytosiphon lomentaria* var. *lomentaria, Chondrus crispus, Hildenbrandia rubra, Polysiphonia harveyi* and *Porphyra umbilicalis*). Some taxa exhibited restricted (<20%) and

Table 3. Summary of seaweed taxa at twenty study sites within the York River Estuary, plus the adjacent open coast at Cape Neddick and Sea Point Maine.

| | NL | SP | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|---|
| Chlorophyta | | | | | | | | | |
| *Blidingia minima* | x | x | x | | | x | | | x |
| *Bryopsis plumosa* | | | | | | | | | |
| *Capsosiphon fulvescens* | | | | | | | | | |
| *Chaetomorpha brachygona* | | x | | | | | | | |
| *Chaetomorpha linum* | x | x | | x | x | | | | x |
| *Chaetomorpha melagonium* | x | x | | | | | | | |
| *Chaetomorpha picquotiana* | | x | | | x | | x | x | x |
| *Cladophora sericea* | x | x | | | | | | | |
| "*Codiolum pusillum*" | | x | | | | | | | |
| *Codium fragile* | | | | | | | | | |
| ssp. *tomentosoides* | x | | | | | | | | |
| *Enteromorpha clathrata* | | | | | | | | | |
| *Enteromorpha flexuosa* | | | | | | | | | |
| ssp. *paradoxa* | x | | | | | | | | |
| *Enteromorpha intestinalis* | x | x | | | | x | x | x | |
| *Enteromorpha linza* | x | | | | | | | | |
| *Enteromorpha prolifera* | x | x | | | | x | | | |
| *Microspora pachyderma* | | | | | | | | | |
| *Monostroma grevillei* | x | x | x | x | | | x | x | x |
| *Monostroma pulchrum* | x | x | | | | | | | |
| *Percursaria percursa* | | | | | | | | | |
| *Prasiola stipitata* | x | | | | | | | | |
| *Rhizoclonium riparium* | x | | | | | | | | x |
| *Rhizoclonium tortuosum* | x | x | | x | x | | | | |
| *Spongomorpha arcta* | x | x | | | | | | | |
| *Spongomorpha spinescens* | x | x | | | | | | | |
| *Ulothrix flacca* | | x | x | | | | x | x | x |
| *Ulothrix speciosa* | | | | | | | x | x | x |
| *Ulva lactuca* | x | x | | | | x | | | x |
| *Ulvaria obscura* | x | x | | | | | x | x | x |
| *Ulvaria oxysperma* | | | | | | | | | |
| *Urospora penicilliformis* | x | x | x | | | x | x | x | x |
| *Urospora wormskioldii* | x | x | | | | | x | | x |
| Total Chlorophyta taxa | 20 | 19 | 4 | 3 | 3 | 5 | 8 | 7 | 11 |
| Mean (±SD) Chlorophyta taxa | (7.9 ± 2.8) | | | | | | | | |
| Phaeophyta | | | | | | | | | |
| *Agarum cribrosum* | x | x | | | | | | | |
| *Alaria esculenta* | x | x | | | | | | | |
| *Ascocyclus distromaticus* | x | | | | | | | | |
| *Ascophyllum nodosum* | x | x | x | x | x | | x | | x |

Table 3. Extended.

| 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | Longevity | %* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| x | | x | | x | x | x | | x | x | x | x | x | Ann. | 68.2 (65) |
| | | | x | | | | | | | | | | Ann. | 4.5 (5) |
| | | | | | | | | | | | | x | Ann. | 4.5 (5) |
| | | | | x | | | | | | | | | Ann.? | 9.1 (5) |
| | | | | x | | | | | | | | | Per. | 27.3 (20) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | x | | | | | | | Per. | 27.3 (25) |
| | | | | | | | x | | | | | | AAnn or PPer. | 13.6 (5) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | x | | | | | | | | | | | | Ann. | 4.5 (5) |
| | | | | | | x | | | | | | | Ann. | 9.1 (5) |
| | | x | x | | | x | x | x | x | x | | x | x | AAnn. | 63.6 (60) |
| | | | | | | | | | | | | | AAnn. | 4.5 (0) |
| | | x | x | | | x | | | | x | x | x | x | AAnn. | 45.5 (40) |
| | | | | | | | | | x | x | | x | | Ann. | 13.6 (15) |
| | x | x | | x | x | x | x | x | x | x | | x | | Ann. | 77.3 (75) |
| | | | | | | | | | | | | | | Ann. | 9.1 (0) |
| | | | | | | | x | | | | | | | AAnn. | 4.5 (5) |
| | | | | | | | | | | | | | | AAnn. | 4.5 (0) |
| | | x | | x | x | | x | x | x | x | | x | x | AAnn. | 50.0 (50) |
| | | | | | | | | | | | | | | AAnn. | 18.2 (10) |
| | x | x | x | | | | | | | | | | | Ann. | 22.7 (15) |
| | | | | | | | | | | | | | | Ann. | 9.1 (0) |
| | | | x | x | x | x | | x | x | | | x | x | Ann. | 59.1 (55) |
| | x | x | x | x | x | x | | x | x | x | | | | Ann. | 54.5 (60) |
| | x | x | | | | | | x | x | x | x | | x | AAnn. or PPer. | 50.0 (45) |
| | x | | | | | | x | x | x | | | | | Ann. | 41.0 (35) |
| | | | | | x | x | x | x | | x | x | x | x | Ann. | 36.4 (40) |
| | x | x | x | x | x | x | x | x | x | x | | x | x | Ann. | 86.4 (85) |
| | x | x | | x | x | | x | x | x | x | | | x | Ann. | 59.1 (55) |
| | 8 | 10 | 7 | 6 | 8 | 10 | 11 | 11 | 12 | 11 | 4 | 10 | 9 | | |
| | | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | | Ann. | 4.5 (0) |
| x | x | x | x | x | x | x | x | x | x | x | x | x | | Per. | 91.0 (90) |

Table 3. Continued.

| | NL | SP | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|---|
| *Ascophyllum nodosum* ecad *scorpioides* | | | | | | x | x | x | |
| *Chorda filum* | x | | | | | | | | |
| *Chorda tomentosa* | x | | | | | | | | |
| *Chordaria flagelliformis* | x | x | | | | | | | |
| *Desmarestia aculeata* | x | x | | | | | | | |
| *Desmarestia viridis* | x | x | | | | | | | |
| *Dictyosiphon foeniculaeus* | x | | | | | | | | |
| *Ectocarpus fasciculatus* | | | x | | | x | | | |
| *Ectocarpus siliculosus* | x | | x | | | x | | | |
| *Elachista fucicola* | x | x | x | | x | x | x | | x |
| *Eudesme virescens* | x | | | | | | | | |
| *Fucus distichus* ssp. *distichus* | x | x | | | | | | | |
| *Fucus distichus* ssp. *edentatus* | x | x | | | x | | | | |
| *Fucus distichus* ssp. *evanescens* | x | x | x | | | | | | |
| *Fucus spiralis* | x | x | | x | | | | | |
| *Fucus vesiculosus* | x | x | x | x | | x | x | x | x |
| *Giffordia granulosa* | | | | | | | | | |
| *Laminaria digitata* | x | x | | | | | | | |
| *Laminaria saccharina* | x | x | | | | | | x | |
| *Laminariocolax tomentosoides* | x | | | | | | | | |
| *Leathesia difformis* | x | | | | | | | | |
| *Mikrosyphar porphyrae* | x | | | | | | | | |
| *Petalonia fascia* | x | x | x | | x | x | x | x | x |
| *Petroderma maculiforme* | | | | | | x | | | |
| *Pilayella littoralis* | x | x | x | | x | x | x | | x |
| *Pseudolithoderma extensum* | | | | | | | | | |
| *Punctaria plantaginea* | x | | | | | | | | |
| "*Ralfsia bornetii*" | | | | | | | | | x |
| *Ralfsia verrucosa* | x | x | | x | x | x | | x | |
| *Sacchorhiza dermatodea* | x | | | | | | | | |
| *Scytosiphon lomentaria* var. *lomentaria* | x | x | x | x | x | x | x | x | x |
| *Sorapion kjellmanii* | | | | | | x | | | |
| *Sphacelaria arctica* | x | | | | | | | | |
| *Sphacelaria cirrosa* | x | | | | | | | | |
| *Spongonema tomentosum* | x | | | | | | | | |
| Total Phaeophyta taxa | 32 | 18 | 10 | 5 | 7 | 11 | 7 | 6 | 7 |
| Mean (±SD) Phaeophyta taxa | (7.0 ± 1.8) | | | | | | | | |
| Rhodophyta | | | | | | | | | |
| *Ahnfeltia plicata* | x | x | | | | | | | |
| *Antithamnionella floccosa* | x | | | | | | | | |
| *Audouinella alariae* | x | | | | | | | | |

Table 3. Extended, continued.

| 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | Longevity | %* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | x | x | x | x | x | x | x | x | x | x | x | x | Per. | 68.2 (75) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| | | | | | | | | | | | | | Ann. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Ann. | 9.1 (0) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| | | | | | | | | | | | | | Ann. | 9.1 (0) |
| | | | | | | | | | | | | | Ann. | 13.6 (10) |
| x | | x | x | | | x | | x | | | | | Per. | 54.5 (50) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | x | | | | | | | | | | | | Per. | 18.2 (0) |
| | x | | | | | | | | | | | | Per. | 18.2 (10) |
| | | x | | | | | | | | | | | Per. | 18.2 (10) |
| x | x | x | x | x | x | x | x | x | x | x | x | x | Per. | 95.5 (95) |
| | | | | | | | | | | | x | | Ann. | 4.5 (5) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 13.6 (5) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| x | x | x | x | x | x | | x | x | x | x | | | Ann. | 81.8 (80) |
| | | x | | | | | | | | x | | | Per. | 13.6 (15) |
| x | x | x | x | x | x | x | x | | x | x | | | Ann. | 77.3 (75) |
| | | | | x | | x | | x | | | | | Per. | 13.6 (15) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| | | | | | | | | | | x | x | | Per.? | 13.6 (15) |
| x | | | | x | | | | x | x | x | | | Per. | 50.0 (45) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| x | x | x | x | x | | | x | | | | x | | Ann. | 72.7 (70) |
| | | | | | | | | | | x | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | | Per.? | 4.5 (0) |
| 7 | 8 | 9 | 7 | 8 | 5 | 6 | 6 | 7 | 6 | 9 | 6 | 3 | | |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | AAnn. | 4.5 (0) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |

Table 3. Continued.

| | NL | SP | I | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|---|
| *Audouinella purpurea* | x | | | | | | | | |
| *Audouinella secundata* | x | | | | | | | x | |
| *Bangia atropurpurea* | x | x | x | | | | | x | x |
| *Bonnemaisonia hamifera* | x | x | | | | | | | |
| *Callithamnion byssoides* | | | | | | | | | x |
| *Callithamnion tetragonum* | | x | | | | | | | |
| *Callocolax neglectus* | x | x | | | | | | | |
| *Callophyllis cristata* | x | x | | | | | | | |
| *Ceramium rubrum* | x | x | | x | | | | | x |
| *Ceramium strictum* | | | | | | | | | |
| *Ceratocolax hartzii* | x | x | | | | | | | |
| *Chondrus crispus* | x | x | x | x | x | x | x | x | x |
| *Clathromorphum circumscriptum* | x | x | | | x | x | | | |
| *Corallina officinalis* | x | x | x | x | x | | | | |
| *Cystoclonium purpureum* | x | x | | | | | | | |
| *Dasya baillouviana* | | | | | | | | | |
| *Dermatolithon pustulatum* | x | x | | | | | | | |
| *Devaleraea ramentacea* | x | | | | | | | | |
| *Dumontia contorta* | x | x | x | x | x | x | x | x | x |
| *Erythrotrichia carnea* | | | | | | | | x | |
| *Fimbrifolium dichotomum* | | x | | | | | | | |
| *Gloisiphonia capillaris* | x | | | | | | | | |
| *Gymnogongrus crenulatus* | x | | | | | | | | |
| *Harveyella mirabilis* | x | | | | | | | | |
| *Hildenbrandia rubra* | x | x | x | x | x | x | x | x | x |
| *Leptophytum laeve* | | | | | | | | | x |
| *Lithophyllum corallinae* | | x | x | | | | | | |
| *Lithothamnion glaciale* | x | x | | | x | x | | | |
| *Lomentaria baileyana* | | | | | | | | | |
| *Lomentaria clavellosa* | | | | | | | | | x |
| *Lomentaria orcadensis* | x | | | | | | | | |
| *Mastocarpus stellatus* | x | x | | x | x | | x | | |
| *Membranoptera alata* | x | x | | | | | | | |
| *Palmaria palmata* | x | x | | | | | | | |
| *Phycodrys rubens* | x | x | | | | | | | |
| *Phyllophora pseudoceranoides* | x | x | | | | | | | |
| *Phyllophora truncata* | x | x | | | | | | | |
| *Phymatolithon laevigatum* | x | x | | | | | | | |
| *Phymatolithon lenormandii* | | | x | | x | | | | |
| *Plumaria plumosa* | x | | | | | | | | |
| *Pneophyllum fragile* | | x | | | | | | | |
| *Polyides rotundus* | x | x | | | | | | | |
| *Polysiphonia denudata* | | | | | | | | | |
| *Polysiphonia flexicaulis* | x | x | | | | | | | |
| *Polysiphonia harveyi* | x | x | | x | x | x | | x | x |

Table 3. Extended, continued.

| 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | Longevity | %* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | | AAnn. | 9.1 (5) |
| | | | | | | | | | | | | | Ann. | 22.7 (15) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | x | | x | x | x | | | Ann. | 22.7 (25) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | x | | | | | | | | | | | Per. | 13.6 (5) |
| | | | | | | | | | | | x | | Per. | 22.7 (15) |
| | | | | | | x | | | | | | x | Ann. | 9.1 (10) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | x | x | | x | x | x | x | x | | x | | Per. | 77.3 (75) |
| | | | | | | | | | | | | | Per. | 18.2 (10) |
| | | | | | | | | | | | | | Per. | 22.7 (15) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | x | | | | x | | | Ann. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | x | x | x | x | x | x | x | x | | x | x | Ann. | 86.4 (85) |
| | | x | | | | | | | | x | x | | Ann. | 18.2 (20) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | | Ann. | 4.5 (0) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | x | x | x | x | x | x | | | x | x | | Per. | 77.3 (75) |
| | | | | | | | | | | | | | Per. | 4.5 (5) |
| | | | | | | | | | | | | | Per. | 9.1 (5) |
| | | | | | | | | | | | | | Per. | 18.2 (10) |
| | | | | | | x | | | | | | | Ann. | 4.5 (5) |
| | | | | | x | | | | | | | | Per.? | 9.1 (10) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | | Per. | 27.3 (20) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | | Per. | 4.5 (0) |
| | | | | | | | | | | | | x | Per. | 9.1 (0) |
| | | | | | | | | | | | | x | Ann. | 4.5 (5) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| x | | | | | x | x | x | x | x | x | | | Ann. | 63.6 (60) |

Table 3. Continued.

| | NL | SP | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|---|
| *Polysiphonia lanosa* | x | x | | x | x | | | | |
| *Polysiphonia nigra* | | | | | | | | | |
| *Polysiphonia nigrescens* | x | | | | | | | x | |
| *Polysiphonia subtilissima* | | | | | | | | | |
| *Polysiphonia urceolata* | x | x | | | | | | | |
| *Porphya amplissima* | x | | | | | | | | |
| *Porphyra linearis* | x | | | | | | | | |
| *Porphyra miniata* | x | x | | | | | | | |
| *Porphyra umbilicalis* | x | x | x | | | x | x | | x |
| *Ptilota serrata* | x | x | | | | | | | |
| *Rhodomela confervoides* | x | x | | | | | | | |
| *Scagelia pylaisei* | x | | | | | | | | |
| *Stylonema alsidii* | | | | | | | | | |
| Total Rhodophyta taxa | 45 | 35 | 8 | 8 | 10 | 7 | 5 | 8 | 10 |
| Mean (±SD) Rhodophyta taxa | (6.5 ± 2.3) | | | | | | | | |
| Grand total seaweed taxa | 97 | 72 | 22 | 16 | 20 | 23 | 20 | 21 | 28 |
| Mean (±SD) total seaweed taxa | (21.4 ± 3.2) | | | | | | | | |

* The two % values represent calculations based upon a total of 22 combined and 20 estuarine stations, respectively.

patchy estuarine distributions (*Chaetomorpha brachygona, Cladophora sericea, Enteromorpha flexuosa* ssp. *paradoxa, Fucus distichus* ssp. *edentatus, F. distichus* ssp. *evanescens, F. spiralis, Laminaria saccharina, Audouinella secundata, Callophyllis cristata* and *Polysiphonia urceolata*), while others were restricted (<20%) to the outer estuary (e.g., *Rhizoclonium tortuosum, Ectocarpus siliculosus, Clathromorphum circumscriptum, Lithophyllum corallinae* and *Lithothamnion glaciale*).

Estuarine taxa also showed various distributional patterns (cf. Table 3). *Ulvaria oxysperma* and *Ascophyllum nodosum* ecad *scorpioides* occurred at 36% and 68% of the sites, respectively. Most taxa either exhibited a restricted (<20%) inner distribution (i.e., *Capsosiphon fulvescens, Microspora pachyderma, Giffordia granulosa, Polysiphonia denudata* and *P. nigra*) or a patchy/restricted (<20%) distribution (e.g., *Bryopsis plumosa, Enteromorpha clathrata, Percursaria percursa, Ectocarpus fasciculatus, Giffordia granulosa, Petroderma maculiforme, Pseudolithoderma extensum, Ralfsia bornetii, Sorapion kjellmanii, Ceramium strictum, Dasya baillouviana, Erythrotrichia carnea, Leptophytum laevae, Lo-*

Table 3. Extended, continued.

| 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | Longevity | %* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| x | | | | | x | | | x | x | x | x | x | Per. | 50 (45) |
| | | | | | | | | | x | x | | | Per.? | 9.1 (10) |
| | | | | | | | x | x | x | | | | Per. | 22.7 (20) |
| | x | | | | | | | | | | | x | Per. | 9.1 (10) |
| | x | | | | | | | | | | | | Per. | 13.6 (5) |
| | | | | | | | | | | | | | Ann. | 4.5 (1) |
| | | | | | | | | | | | | | Ann. | 4.5 (1) |
| | | | | | | | | | | | | | Ann. | 9.1 (0) |
| | x | | x | | x | | x | x | x | x | | x | x | Ann. | 68.2 (65) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | Per. | 9.1 (0) |
| | | | | | | | | | | | | | AAnn. | 4.5 (0) |
| | | | | | | | | x | | | | | Ann. | 4.5 (5) |
| | 9 | 3 | 3 | 3 | 4 | 6 | 10 | 5 | 6 | 8 | 7 | 4 | 5 | | |
| 24 | 21 | 19 | 16 | 20 | 21 | 27 | 22 | 25 | 25 | 20 | 20 | 17 | | | |

*mentaria baileyana, L. clavellosa, Phymatolithon lenormandii* and *Polysiphonia subtilissima*).

## FLORISTIC COMPARISONS

Figure 6 compares species richness patterns in the York River Estuary with two nearshore open coastal sites (Cape Neddick and Sea Point) and twelve other estuarine habitats in southern Maine, New Hampshire and Massachusetts. Ninety-five taxa were recorded at Cape Neddick, while Sea Point and the York River Estuary both had 72 taxa, albeit their species compositions were very different. A comparison of the York, Great Bay, Hampton-Seabrook and Merrimack River Estuaries suggests an intermediate pattern of species richness (Figure 6). A "typical" estuarine reduction pattern (cf. Mathieson and Penniman, 1991) is evident within the ten primary subareas of the Great Bay Estuary System (Table 1), ranging from the Piscataqua River (143 taxa), Little Bay (130 taxa), Great Bay (90 taxa), and inner riverine sites like the Salmon Falls (16 taxa) and Winnicut Rivers (4 taxa). The York River has a more diverse flora than the Hampton-Seabrook Estuary (63 taxa) or the tidal waters of the Merrimack River (25

taxa). Thus, the York River has its greatest affinities to several mid-estuarine habitats within the Hampton-Seabrook and Great Bay Estuaries (Table 1). A comparison of the number and percentage of York River taxa within these same open coastal and estuarine sites confirms many of the above described patterns (cf. Figure 6). The greatest floristic affinities were between the York and Piscataqua Rivers (i.e., 68 taxa and 94%), followed by Little Bay (63 and 88%), Great Bay (52 and 72%) and the Hampton-Seabrook Estuary (41 and 57%). By contrast, the York River showed reduced affinities with the Merrimack River (20 taxa and 28%), as well as a variety of inner estuarine sites (e.g., Winnicut River, 4 taxa and 5.5%). The York River only shares a modest number of taxa with the nearby coastal sites at Cape Neddick (42 and 58%) and Sea Point (41 taxa and 57%).

The numbers of seaweed taxa at each site within the York River Estuary, plus those at Cape Neddick and Sea Point, are illustrated in Figure 7 and Table 3. Overall, patterns of species richness within the estuary were irregular and reduced in numbers. A total of 16–28 taxa per site were recorded within the York River (mean = 21.4 ± 3.2 taxa), while Cape Neddick and Sea Point had 95 and 72 taxa, respectively. A comparison of the mean number of taxa per site within the York River and twelve other estuarine habitats is given in Figure 8. The York River is comparable to the Piscataqua River (mean = 25.3 ± 24.9) and Great Bay (mean = 22.5 ± 18.0), while it is lower than Little Bay (mean = 34.1 ± 29.0). By contrast, the York River has a greater number of taxa per site than several mid- and inner-estuarine areas like the Oyster (mean = 12.6 ± 7.9) and Winnicut Rivers (mean = 1.3 ± 1.6). It is also more diverse than the Hampton-Seabrook (mean = 10.5 ± 5.5) and Merrimack River Estuaries (mean = 3.5 ± 5.2). Thus, the York River is more spatially consistent (mean = 21.4 ± 3.2) than the Piscataqua River, Little Bay and Great Bay, and is analogous to several inner-estuarine sites like the Cocheco (±4.3) and Salmon Falls Rivers (±3.4)—albeit the species richness within the latter rivers is much lower than in the York River (Table 3).

## LONGEVITY PATTERNS

Of the 131 taxa recorded from the York River, Cape Neddick and Sea Point, 62 were annuals (47%), 67 (51%) perennials and

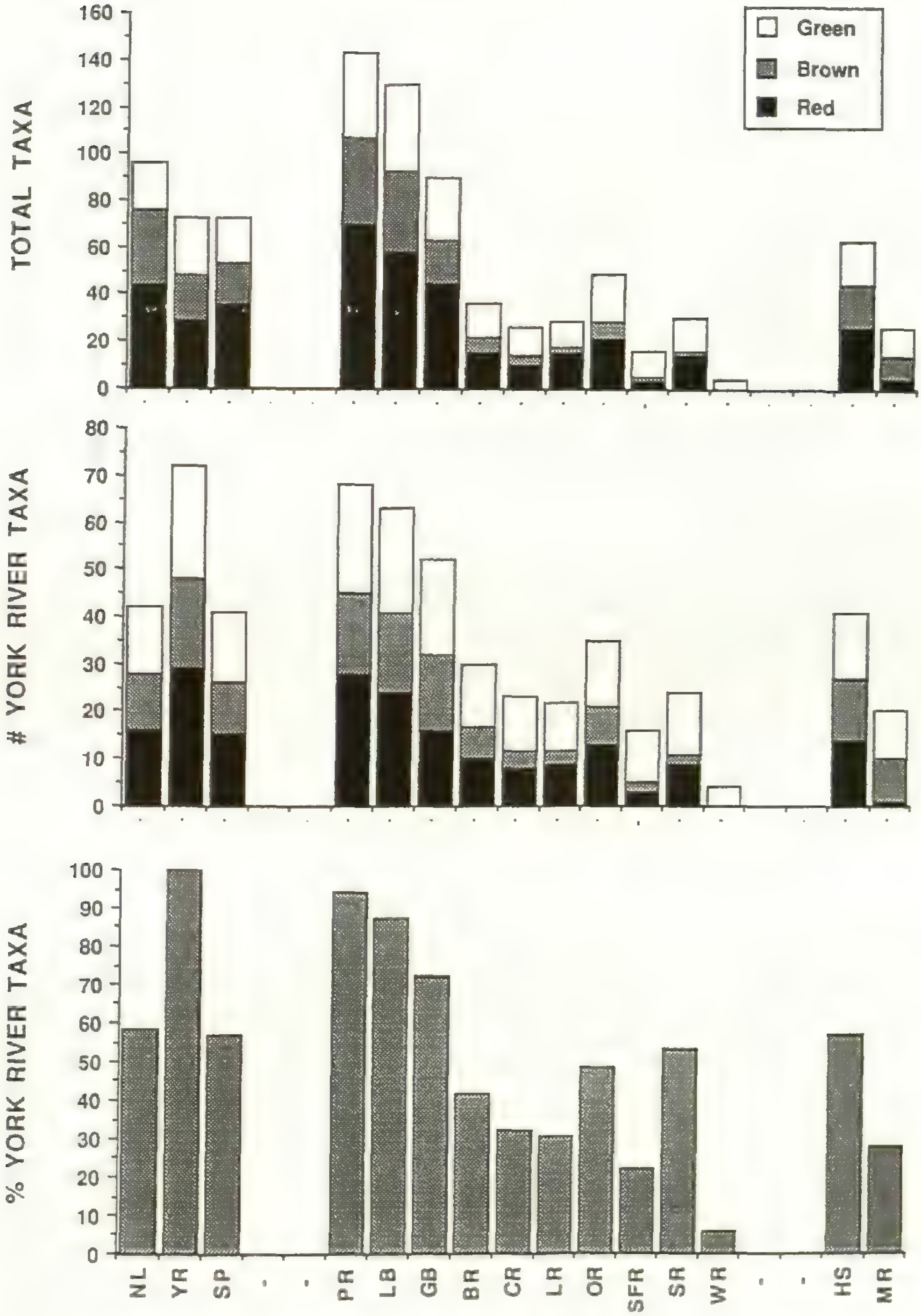


Figure 6. A comparison of the York River estuarine flora with sixteen other coastal and estuarine habitats, expressed as the total number of seaweed taxa/site (green, brown and red), as well as the number and percentage of York River taxa in common. See Table 1 and Appendix I for habitat descriptions. Abbreviations: NL (Nubble Lighthouse or Cape Neddick), YR (York River Estuary), SP (Sea Point), PR (Piscataqua River), LB (Little Bay), GB (Great Bay), BR (Bellamy River), CR (Cocheco River), LR (Lamprey River), OR (Oyster River), SFR (Salmon Falls River), SR (Squamscott River), WR (Winnicut River), HS (Hampton-Seabrook Estuary) and MR (Merrimack River Estuary).

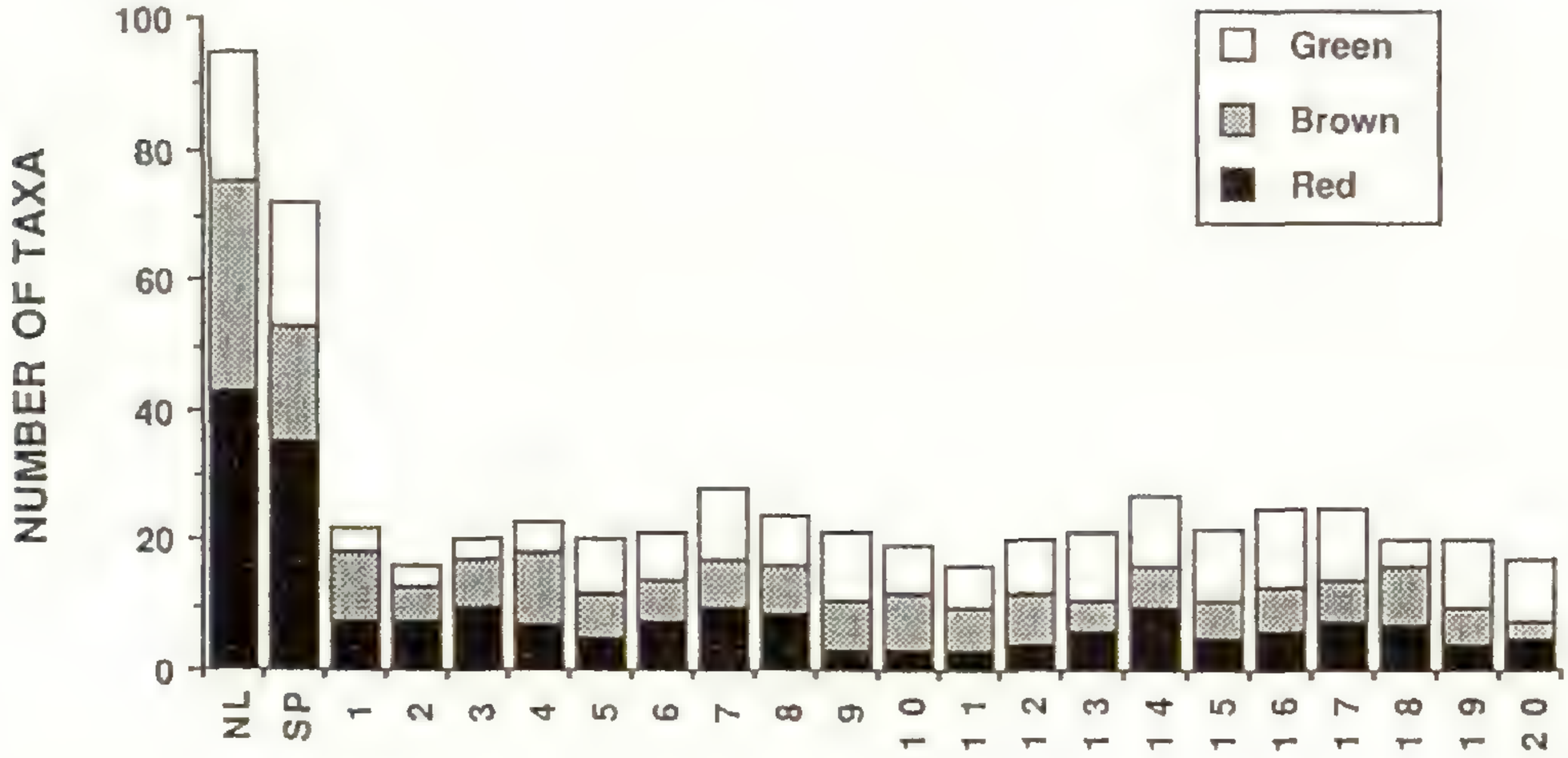


Figure 7. Total number of seaweed taxa/site (green, brown and red) at twenty York River estuarine sites and two adjaent open coastal sites (Cape Neddick and Sea Point, Maine).

2 (2%) either aseasonal annuals or pseudoperennials (Figure 5, Table 3). Overall, the green algae exhibited the highest percentage of annuals (81% or 25 taxa), the browns were intermediate (46% or 18 taxa) and the reds had the lowest number (31% or 19 taxa).

## DICUSSION

As noted by Mathieson and Penniman (1991) the physical extremes inherent within estuaries may determine the distributional limits of species where their physiological tolerances are approached (Fralick and Mathieson, 1975; Guo and Mathieson, 1992; Kinne, 1970, 1971; Penniman and Mathieson, 1985). Wilkinson (1980) describes an analogous pattern, citing varying ecological requirements between inner and outer estuarine floras in Great Britain, with the species of the inner estuary comprising a group having wide ecological tolerances, while those with more limited environmental ranges are at an advantage in less harsh conditions of the outer estuary. Such differences in ecological requirements between inner and outer estuarine floras are evident within the York River (Figure 5), Great Bay (Mathieson et al., 1981; Mathieson and Penniman, 1986b) and Hampton-Seabrook Estuaries (Mathieson and Fralick, 1972). The inner estuarine species include seasonally dynamic warm temperate or "mixed floras" (i.e., annuals), while those of the outer estuary are dominated by a separate cold-temperate, perennial-dominated flora (Mathie-

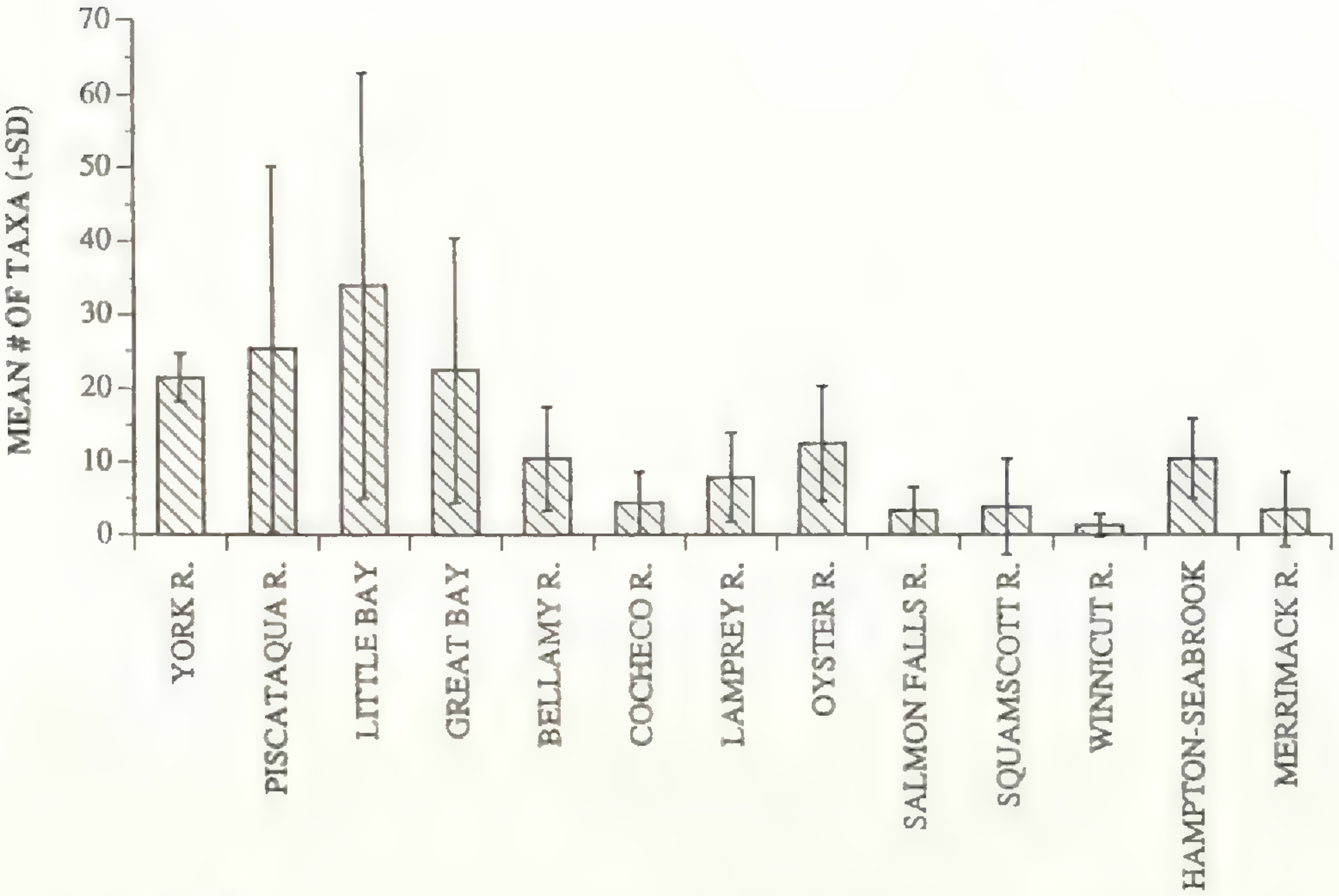


Figure 8. Mean (±SD) number of green, brown and red algal taxa/site within the York River Estuary and fourteen other geographical areas. See Table 1 for a synopsis of number of collection sites/area.

son, 1978; Mathieson and Hehre, 1986). Aside from such hydrographic variability, a conspicuous reduction in the amount of rocky substrata is present upstream within the York River Estuary. A combination of both physical factors probably causes gross fluctuations in numbers of taxa per site, a general reduction in the number of species upstream and the ultimate dominance of riverine habitats by ephemeral Chlorophyceae (Coutinho and Seeliger, 1984; Josselyn and West, 1985; Ketchum, 1983; Mathieson and Penniman, 1986b; Wilkinson, 1980).

Several specific examples of limited rocky substrata can be cited. Foremost, the upper reaches of the York River are composed of steep channels and dissected saltmarshes, which have a limited flora dominated by *Blidingia minima, Enteromorpha* spp., *Ulva lactuca, Urospora* spp., *Ulothrix* spp., *Ulvaria* spp., *Rhizoclonium riparium, Fucus vesiculosus, Ascophyllum nodosum* and *A. nodosum* ecad *scorpioides.* Many of the latter taxa occur as unattached or entangled masses (Norton and Mathieson, 1983). For example, the marsh ecad *scorpioides* of *A. nodosum* grows abundantly at diverse sites (Table 3), forming entangled masses amongst *Spartina alterniflora.* By contrast, only a single detached

marsh ecad of *F. vesiculosus* was found at station 16 where it grew as a partially embedded fragment (Appendix 1, Table 3). The morphology and proliferous habitat of the latter plant are similar to *F. vesiculosus* megecad *limicola* (Baker and Bohling, 1916). Although marsh ecads of *F. vesiculosus* are common in Europe (cf. Norton and Mathieson, 1983), they are uncommon and sporadically distributed in New England (Chapman, 1939).

Distributional patterns of several epiphytic algae (e.g., *Elachista fucicola, Pilayella littoralis, Callithamnion byssoides, Ceramium rubrum* and *Polysiphonia lanosa*) paralleled the occurrence of the two dominant canopy fucoids, *Ascophyllum nodosum* and *Fucus vesiculosus* (cf. Table 3), presumably because of reduced availability of rocky substratum. The occurrence of epiphytic *F. vesiculosus* on *A. nodosum* ecad *scorpioides* at two sites (i.e., 7 and 14) should also be noted, as we know of no other records of its occurrence on the ecad. Epiphytic *Fucus* may occasionally grow on attached *A. nodosum,* particularly on isolated rock outcrops within estuarine mudflats such as in Great Bay, New Hampshire (A. Mathieson, unpubl. data). Patchy distributional patterns of several attached taxa on scattered rock outcrops should also be noted, including *Ectocarpus* spp., *Laminaria saccharina, Bangia atropurpurea, Corallina officinallis, Clathromorphum circumscriptum, Leptophytum laeve, Lithophyllum corallinae, Lithothamnion glaciale, Phymatolithon lenormandi and Mastocarpus stellatus* (Table 3). Lastly, the restricted estuarine occurrence of *Callophyllis cristata* on *Littorina littorea* at station 8 (1.6 miles inland) may have been due to its host's migration from the open coast.

A comparison of the York, Piscataqua and Merrimack Rivers is instructive as all three are outer estuarine habitats with contrasting floras (cf. Mathieson and Fralick, 1972, 1973; Mathieson and Penniman, 1986b; Mathieson et al., 1981). Open coastal species drop out after approximately 1.0 mile on the Merrimack versus 2–3 miles on the York (cf. Table 3) and approximately 8.5 miles on the Piscataqua River (Reynolds and Mathieson, 1975; Mathieson et al., 1983). The latter site on the Piscataqua River (i.e., Dover Point) has strong tidal currents (approx. 5 knots) and diverse rocky substrata. A comparison of temperature and salinity conditions within the York River (cf. Figures 3 and 4) shows that they are comparable to those found at Dover Point (i.e., −2.0 to 24.1°C and .9 to 30.3‰), while hydrographic variability (particularly salinity and siltation) is maximal on the Merrimack (cf.

Mathieson and Fralick, 1973; Miller et al., 1971). The Merrimack River has the most depauperate flora (only 25 taxa), the York is intermediate (72 taxa) and the Piscataqua the most diverse (144 taxa). Several adverse physical factors (cf. above), as well as domestic and industrial pollution, are probably responsible for the reduced diversity of the Merrimack River. Besides being one of the most polluted rivers in New England (cf. Anonymous, 1984, 1987; Jerome et al., 1965; Lyons et al., 1982; Mathieson and Fralick, 1973; Miller et al., 1971), the Merrimack is also one of the largest sources of freshwater discharge into the Gulf of Maine (Apollonio, 1979). As noted by several investigators (Clokie and Boney, 1980; Daly and Mathieson, 1977; Edwards, 1972; Littler, 1980; North et al., 1964; Patrick, 1963, 1964, 1973; Round, 1981; Wilkinson, 1980), patterns of low species diversity are typical responses to stress, often allowing only a few tolerant species to dominate in both numbers and biomass. For example, the abundance of many ulotrichalean green algae, such as *Ulva lactuca*, *Enteromorpha* and *Ulvaria* (*Monostroma*) spp., typifies many eutrophied estuarine habitats (Cotton, 1910; Fritsch, 1935; Sawyer, 1965). The latter species are not only tolerant of extremes of pollution but of gross fluctuation in hydrographic conditions. While industrial development and eutrophication are limited on the York River (cf. above), they are intermediate on the Piscataqua and highest on the Merrimack (Mathieson and Penniman, 1991). Aside from these contrasting patterns, the Piscataqua River also has the greatest diversity of habitats (e.g., tidal rapids, saltmarshes, boulders, cobbles, shingle, etc.) and stable substrata.

Josselyn and West (1985) compare species richness within several estuaries, including San Francisco Bay and Great Bay. Beyond the mouth of the former site a relatively low number of taxa occurs upstream (i.e., 21–61 taxa/site). Similar patterns of low species richness are known from several other estuaries with high sedimentation and limited solid substrata, including the York, various subsets of the Great Bay and Hampton-Seabrook Estuaries (Figure 8), the Chesapeake Bay (Mathieson and Fuller, 1969; Orris 1980), several British and Dutch estuaries (Hartog, 1967; Nienhuis, 1975; Wilkinson, 1980), and several Icelandic fjords (Munda, 1969, 1978). Within such turbid habitats there is a relatively small pool of common estuarine species (Munda, 1969, 1972; Orris, 1980; Wilkinson, 1980). For example, Orris (1980) lists 62 taxa from the upper reaches of the Chesapeake Bay in

Maryland, with *Cladophora, Enteromorpha, Ulva, Ceramium* and *Polysiphonia* being most frequent.

A comparison of the species richness within the York River and the Great Bay Estuary System (i.e., all ten subareas in Figure 6) also showed pronounced differences, with 72 and 168 taxa occurring at the two sites, respectively. As noted above, such contrasting patterns are probably due to a variety of factors, including habitat diversity, hydrographic stability, pollution, availability of rocky substrata, etc. (Murray and Littler, 1989; Murray et al., 1980). With the exception of the crustose brown alga *Sorapion kjellmanii,* all of the taxa recorded from the York River are known from the Great Bay Estuary (Mathieson and Hehre, 1986). By contrast, a greater number of freshwater, coastal and estuarine taxa are known from the Great Bay Estuary than the York River. Several of these estuarine taxa represent disjunct "southerly" plants (Bird et al., 1976; Mathieson and Hehre, 1986; Novaczek et al., 1987) that are either absent (e.g., *Chondria baileyana, Gracilaria tikvahiae, Polysiphonia elongata*) or rare within the York River (e.g., *Bryopsis plumosa, Ceramium strictum, Dasya baillouviana, Lomentaria baileyana, Polysiphonia denudata* and *P. subtilissima*). A similar pattern exists within the Hampton-Seabrook Estuary: the absence of many "southerly" taxa and a dominance of saltmarshes (Mathieson and Fralick, 1972). Presumably these warm water plants are either unable to grow and/or compete with other saltmarsh-inhabiting taxa. The vast subtidal mudflats of the Great Bay Estuary may be some of the most suitable habitats for such warm water taxa in northern New England; these habitats are essentially absent from the York and Hampton-Seabrook Estuaries, except near outer estuarine sites where water temperatures are too low for optimal growth and/or survival (Figure 4; see also Fralick and Mathieson, 1975; Guo and Mathieson, 1992; Novaczek et al., 1987).

Although this study has primarily dealt with the algal flora of the York River Estuary, our coastal collections have documented two new records from southern Maine and New Hampshire. Foremost, the "arctic" taxon *Porphyra amplissima,* as recently defined by Bird and McLachlan, 1992, has been recorded from Cape Neddick (Table 3). Previously it was included under *P. miniata* (Taylor, 1957). An evaluation of herbarium specimens at Harvard University (FH) and the University of New Hampshire (NHA) has

documented its presence from several open coastal sites in Maine, as well as nearshore and estuarine sites within New Hampshire (Hehre and Mathieson, 1993). Some of these samples date to ca. 1880. The presence of *P. amplissima* near the mouth of the York River suggests it may be found within this habitat as well. Recent expansion of the "alien" species *Codium fragile* ssp. *tomentosoides* (Van Patten, 1992) should also be noted (Mathieson and Hehre, 1986). It was initially found at Cape Neddick in November of 1989 and is now abundant at the Isles of Shoals (particularly on Appledore and Smuttynose Islands, Maine). One attached specimen was recently found on the nearshore open coast of New Hampshire at Jaffrey Point, Newcastle (September, 1992), while drift specimens were collected during the same period at nearby Rye Ledge (Rye, New Hampshire) and within the inner reaches of the Great Bay Estuary (Weeks Point). Further expansion of its distributional range may provide a variety of problems (Van Patten, 1992).

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Appendix 1. York River estuarine and adjacent open coastal study sites (Cape Neddick and Sea Point) in southern Maine.

| Station | Miles from coast | Longitude | Latitude | Description |
|---|---|---|---|---|
| Open Coastal | | | | |
| NL | 0.0 | 70°35′25″W | 43°09′56″N | Nubble Light, Cape Neddick, Maine; an exposed site with substrata primarily consisting of massive rock outcrops |
| SP | 0.0 | 70°30′32″W | 43°05′26″N | Sea Point, Kittery, Maine; semi-exposed site with substrata consisting of boulders (cobbles), rock outcrops and sand |
| York River | | | | |
| 1 | 0.0 | 70°37′36″W | 43°08′06″N | Cove between Roaring Rock Point and Cow Beach Point; mostly rocky but some sand and gravel habitats also present |
| 2 | 0.4 | 70°38′12″W | 43°07′18″N | South bank of river, across from Stage Neck; a rocky habitat with limited mudflats |
| 3 | 0.4 | 70°38′25″W | 43°07′26°N | North bank of river by Stage Neck Condominiums; a rocky habitat with boulders and rock outcrops |
| 4 | 0.8 | 70°38′45″W | 43°07′31″N | South bank of river, just north of the new Rte. 103 bridge; a variety of habitats including mudflats, saltmarsh and some rocks |
| 5 | 0.8 | 70°38′32″W | 43°07′44″N | North bank of river at new Rte. 103 bridge; habitats include mudflats, rocks and saltmarshes traversed by many drainage ditches |
| 6 | 1.0 | 70°39′00″W | 43°07′49″N | North bank of river between Sewall Bridge and Rte. 103 bridge; substratum varied, including mudflats, sand, cobbles and boulders; fast-flowing water draining into York River from Barrells Millpond |
| 7 | 1.2 | 70°39′07″W | 43°07′42″N | North bank of river at Sewall Bridge; substrata consisting of mudflats and saltmarsh |
| 8 | 1.6 | 70°39′45″W | 43°07′56″N | North bank of river at Sewall Bridge, upstream from #7; substrata mainly consisting of sand, gravel, and some limited saltmarsh with scattered small rocks |

Appendix 1. Continued.

| Station | Miles from coast | Longitude | Latitude | Description |
|---|---|---|---|---|
| 9 | 2.0 | 70°40′32″W | 43°07′52″N | North bank of river, midway between Sewall Bridge and Ramshead Point; extensive mudflats with rock outcrops and a narrow band of saltmarsh |
| 10 | 2.4 | 70°40′25″W | 43°07′37″N | South bank of river on River Meadow Lane; just south of Ramshead Point; extensive mudflats |
| 11 | 2.4 | 70°40′15″W | 43°07′50″N | North bank of river approaching Ramshead Point; substrata consisting of rock outcrops, large boulders, saltmarshes and mudflats |
| 12 | 2.6 | 70°40′45″W | 43°08′04″N | North bank of river, just opposite Ramshead Point; near a private dock with boulders and cobbles, as well as mudflats and saltmarshes |
| 13 | 2.8 | 70°41′10″W | 43°07′56″N | North bank of river, just downstream from Rice's Bridge on Rte. 1; some rocky areas but mostly mudflats with some saltmarsh |
| 14 | 3.4 | 70°43′30″W | 43°07′51″N | South bank of river, at Rice's Bridge on Rte. 1; substrata primarily consists of mudflats and saltmarsh, with some scattered rocks; two outfall pipes present |
| 15 | 3.4 | 70°41′25″W | 43°08′13″N | North bank of river, at I-95 bridge; extensive mudflats and very limited saltmarsh; rocks and cobbles occur at bridge pilings |
| 16 | 3.6 | 70°41′45″W | 43°08′18″N | Mouth of Cider Hill Creek (north bank) just above the I-95 bridge; extensive mudflats with scattered rocks and some saltmarsh |
| 17 | 4.0 | 70°42′05″W | 43°08′32″N | Mouth of Boulter Pond Creek (north bank) between I-95 and Scotland Bridge; substrata primarily consisting of mudflats and saltmarsh |
| 18 | 4.2 | 70°42′30″W | 43°08′50″N | Just downstream from Scotland Bridge (north bank); a mudflat area with very little saltmarsh |
| 19 | 4.4 | 70°43′15″W | 43°09′01″N | North bank of river, at Scotland Bridge on Scotland Bridge Road; substrata primarily consisting of |

Appendix 1. Continued.

| Station | Miles from coast | Longitude | Latitude | Description |
|---|---|---|---|---|
| | | | | mudflats, saltmarsh and bridge pilings |
| 20 | 4.7 | 70°43′30″W | 43°09′12″N | North bank of river, near a large farm—upstream from Scotland Bridge on Rte. 91; substrata primarily consisting of mudflats and some saltmarsh |

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# TAXONOMIC STUDIES IN THE MICONIEAE (MELASTOMATACEAE). V. *MICONIA STENOBOTRYS*, CIRCUMSCRIPTION AND RELATIONSHIPS

WALTER S. JUDD AND ELIZA KARPOOK

**ABSTRACT**

*Miconia stenobotrys*, a member of section *Chaenopleura*, is considered to constitute a species from a phenetic as well as a phylogenetic standpoint. It occurs widely in the Cordillera Central/Massif du Nord of Hispaniola, growing mainly in forests dominated by *Pinus occidentalis*. The species is circumscribed broadly, including *M. azuensis*, *M. artibotinensis*, *M. buchii*, and *M. leptoneura*, as well as populations with very prominently 4-flanged stems from the Parque Nacional José del Carmen Ramírez/Loma la Vieja region of the Dominican Republic. A revised description and an illustration are provided, and a list of specimen citations is presented. *Miconia stenobotrys* is distinguished from its presumed closest relatives, i.e., *M. krugii*, *M. samanensis*, and *M. zanonii*, by its falcate leaves that are slightly to strongly V-folded along the midvein and distinctive elongated inflorescences. It is quite variable in several morphological features, especially in extent of development of U-shaped stem flanges, number of multicellular, long-stalked, gland-headed hairs on the stems and leaves, degree of toothing of the leaf margin, placement of secondary veins of the lamina, and flower size. However, no phenetic discontinuities were discerned among analyzed specimens, and the above listed characters often vary within populations.

Key Words: *Miconia stenobotrys*, *Miconia* sect. *Chaenopleura*, Melastomataceae, phylogenetic species concept

## INTRODUCTION

In the course of field work in connection with a taxonomic revision of *Miconia* section *Chaenopleura* Benth. & Hook. and a floristic treatment of Melastomataceae for the Flora of Hispaniola a diverse array of populations representing a species (or several related species), i.e., the *Miconia stenobotrys* complex, was collected. These plants, easily recognized by their leaves that are falcate and slightly to strongly V-folded along midvein and their distinctive elongated cymose inflorescences, are referable to *Miconia* sect. *Chaenopleura* (see Cogniaux, 1891; Judd and Skean, 1991). The West Indian members of section *Chaenopleura* form a distinctive, diverse, and presumably monophyletic group, which may be diagnosed by the possession of an actinomorphic androecium, that is, the stamens form a radially symmetrical pattern

around style (instead of being deflexed to one side of flower). The stamens are white and glabrous, and the obovate anthers each open by two longitudinal slit-like pores. The group is also characterized by globose fruits that turn from red to blue (or blue-white) at maturity and angular-obovoid seeds with a more or less smooth testa (see Judd and Skean, 1991, figure 10B). Fifty-six Antillean species of *Miconia* sect. *Chaenopleura* have been (or are in the process of being) described. As discussed herein, some of these appear to be synonymous with other species. A few undescribed species, however, recently have been discovered (Judd, unpubl. data), and the group likely is represented by ca. 50 species in the Greater Antilles (see Judd and Beaman, 1988; Judd and Skean, 1987; Judd et al., 1988; Judd and Skean, submitted a and b; Liogier and Martorell, 1982; León and Alain, 1957; Moscoso, 1943; Proctor *in* Adams, 1972).

Specific limits among the populations comprising the *Miconia stenobotrys* complex have been especially troublesome, with some botanists recognizing several species, i.e., *M. stenobotrys, M. azuensis, M. buchii, M. artibotinensis,* and *M. leptneura* (Cognaux *in* Urban, 1908; Urban and Ekman *in* Urban, 1929; Moscoso, 1943) and others (in herbarium identifications) applying the names *M. azuensis* or *M. stenobotrys* more broadly. *Miconia stenobotrys* is here re-circumscribed broadly and a detailed description and an illustration are provided. Its infraspecific pattern of variation is assessed through traditional taxonomic procedures, i.e., a survey of numerous populations based on field-studies and herbarium material, and a Principal Components Analysis (PCA). The species is characterized eco-geographically and a list of specimen citations is presented. *Miconia stenobotrys,* as re-circumscribed, is compared with several closely related species, and its phylogenetic relationships are assessed briefly.

## MEASUREMENTS/HERBARIUM CITATIONS

All measurements (except for plant height, flower and fruit color, which were taken from information given on specimen labels or observed in the field, or floral and fruit measurements, which were taken from liquid-preserved or rehydrated material) included in the species descriptions come directly from dried herbarium material. The inflorescence length was measured from terminal flower to point at which first branch-pair emerges from

axis, and the peduncle is defined as the internode separating cyme from uppermost leaf pair. The two or more prominent veins running in convergent arches toward the leaf apex are termed secondary veins since they clearly branch from the midvein. The detailed description has a format similar to that of other descriptions published as part of a series of taxonomic studies in the Miconieae, which allows for easy comparison; see Judd and Beaman (1988), Judd and Skean (1987), Judd et al. (1988), and Judd and Skean (submitted a and b).

In the citation of specimens, abbreviations of institutions follow the eighth edition of *Index Herbariorum* (Holmgren et al., 1990).

## PHENETIC STUDIES

*Miconia stenobotrys,* as traditionally delimited, consistently has been confused with several phenetically similar "species," i.e., *M. azuensis, M. buchii, M. artibotinensis,* and *M. leptoneura.* In addition, a population of plants clearly belonging within the *Miconia stenobotrys* complex, but with 4-flanged stems, i.e., two flanges extending below each point of petiole attachment and joining to form a conspicuous, U-shaped flange ca. 1–2 mm broad at the adjacent lower node, recently has been discovered in the Dominican Republic, prov. San Juan, near the "Forestry House" above Los Fríos, in the Parque Nacional José del Carmen Ramírez; see *García 1245, Judd 6693, 6694, 6698, Skean 3269.* Somewhat similar plants were collected by Eric Ekman on the nearby Loma la Vieja, i.e., *Ekman H13410* and *H13441.* Typically, the twigs of *M. stenobotrys* (or the other species listed above) are square to rectangular in cross-section, but more or less lack flanges. The phenetic separation between the above listed species of the *Miconia stenobotrys* complex, along with the plants with conspicuously 4-flanged stems, was evaluated by a Principal Components Analysis of 114 flowering or fruiting shoots representing the full range of observed variation; see discussion of this technique in Sneath and Sokal (1973) and Wiley (1981). This analysis employed the CLUSTAN mainframe computer program, version 3.2 (Wishart, 1987). Variation in 12 continuously varying or "count" characters of leaf, stem, and inflorescence morphology (Table 1) was scored for each specimen and the taxa ordinated along the first two principal components (Figure 1). These characters show variation among populations of the *Miconia steno-*

Table 1. Characters used in PCA of *Miconia stenobotrys* complex. (All node and leaf measurements taken at third node below cyme.)

1. Petiole length
2. Lamina length
3. Lamina width
4. Distance between base of lamina and point at which major secondary veins join with midvein
5. Distance between major secondary veins and leaf margin (as measured at lamina midpoint)
6. Number of teeth per 2 cm (centered at lamina midpoint)
7. Length of largest tooth (located at any point along leaf margin)
8. Flange width (measured at widest point)
9. Number of multicellular, long-stalked, gland-headed hairs per internode
10. Inflorescence length
11. Pedicel length
12. Basal inflorescence branch length

*botrys* complex, and several have been used in specific delimitations within the group (*see* Cogniaux *in* Urban, 1908; Urban and Ekman *in* Urban, 1929). The resulting diagram (Figure 1), describing 60% of the variation contained in the original data set, indicates that there are no phenetic discontinuities among analyzed specimens, although some divergence is evident between specimens from the Jarabacoa–Constanza/El Rubio regions, the Lagunas de Cenobí–La Cidra–La Leonor/Hinche regions, the Parque Nacional José del Carmen Ramírez–El Frío region, and the Morne Belance region. Plants of the Río Maguá region (as represented by *Valeur 736*), the Restauración–Río Artibonito region and populations to the west in Haiti (e.g., *Ekman H3396, Ekman H6275*), and Loma la Vieja region (as represented by *Ekman H13440, Ekman H13441*) are more or less intermediate between the phenetically divergent populations of the Constanza–Jarabacoa and the Lagunas de Cenobí–La Cidra–La Leonor regions (*see* Figures 1 and 2). The strongly stem-flanged plants of the Parque Nacional José del Carmen Ramírez–El Frío region, although distinctive, show an overlapping pattern of phenetic variation with plants of the Lagunas de Cenobí–La Cidra–La Leonor region, the Hinche region, and the Loma la Vieja region (Figure 1). Considerable variability is present, but no correlated character states were found that could be used to delimit the members of this complex into two or more phenetically delimited species. Variation is present in all of the characters included in Table 1

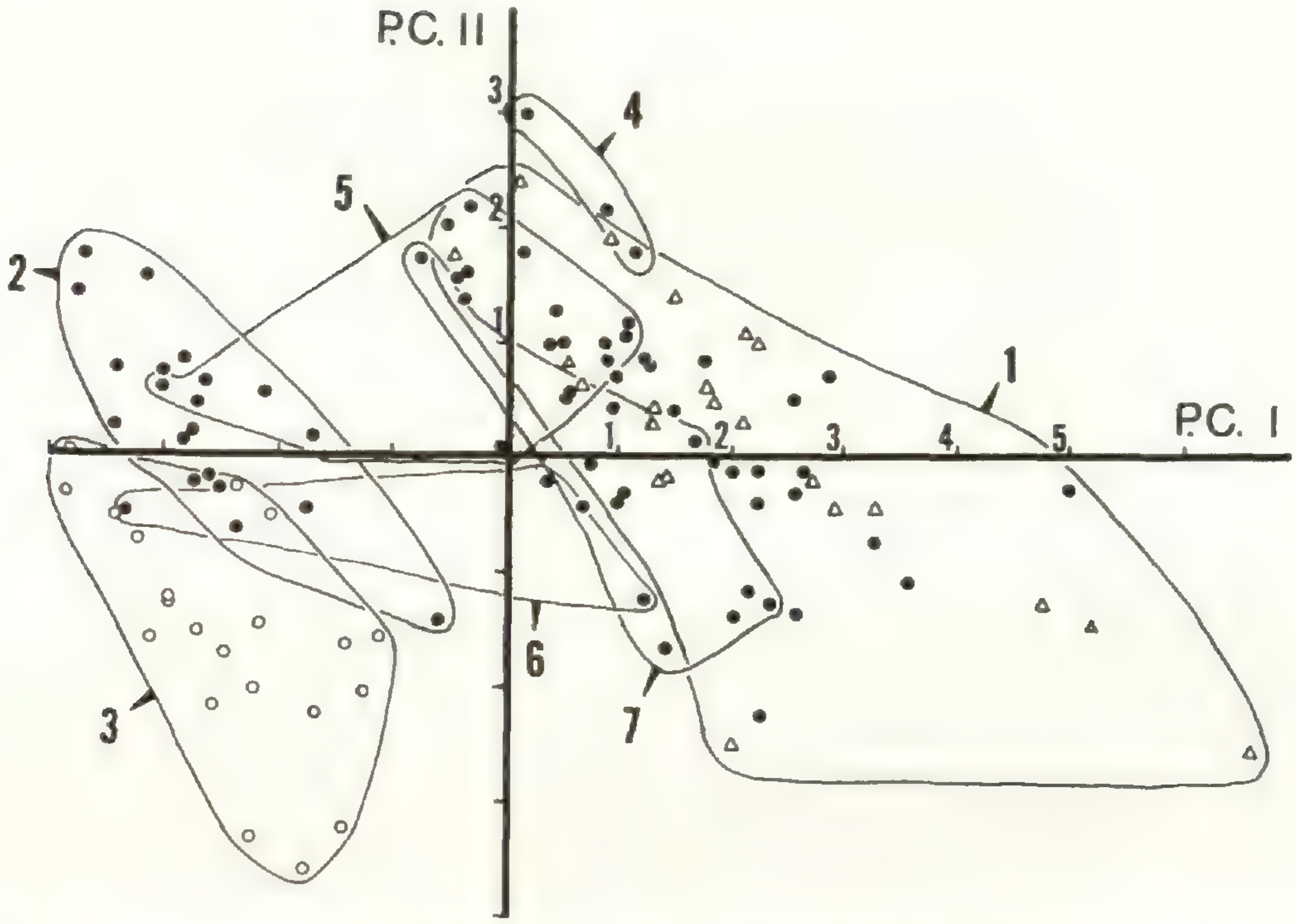



Figure 1. Plot of the first two principal components resulting from phenetic analysis of *Miconia stenobotrys* complex of Hispaniola. PC I describes 45% of the variation; PC II describes 15% of the variation. Circles = specimens collected in the Parque Nacional José del Carmen Ramírez–El Frío region, i.e., *Judd 6693, 6694, 6698, & García 1245*; triangles = specimens collected by *Judd* in the Constanza–Jarabacoa region, i.e., *2955, 5125, 5143, 6626, 6627, 6629, 6653, 6659*; dots = other specimens. Circled dots indicate variation expressed by plants of a particular geographical region: 1 = Constanza–Jarabacoa region; 2 = Lagunas de Cenobí–La Cidra–La Leonor–Hinche region; 3 = Parque Nacional José del Carmen Ramírez-El Frío region; 4 = Morne Belance region; 5 = Río Maguá region; 6 = Loma la Vieja region; and 7 = Restauración–Río Artibonito region.

(see description), but is especially remarkable in extent of flange development (stems lacking flanges to conspicuously 4-flanged), marginal condition (leaves entire to clearly serrate, and teeth with or without long-stalked gland-headed hairs), indumentum (stems and leaves with multicellular, long-stalked, gland-headed hairs, or such hairs lacking), and placement/number of secondary leaf veins (2 or 4, placed ca. .7–6 mm in from margin, and ± basal to strongly suprabasal). Although not included in the phenetic analysis, flower size is also quite variable, especially the length of the petals and internal calyx lobes. (As with the vegetative and inflorescence characters, floral features show more or less continuous variation among populations.) Certain character states are

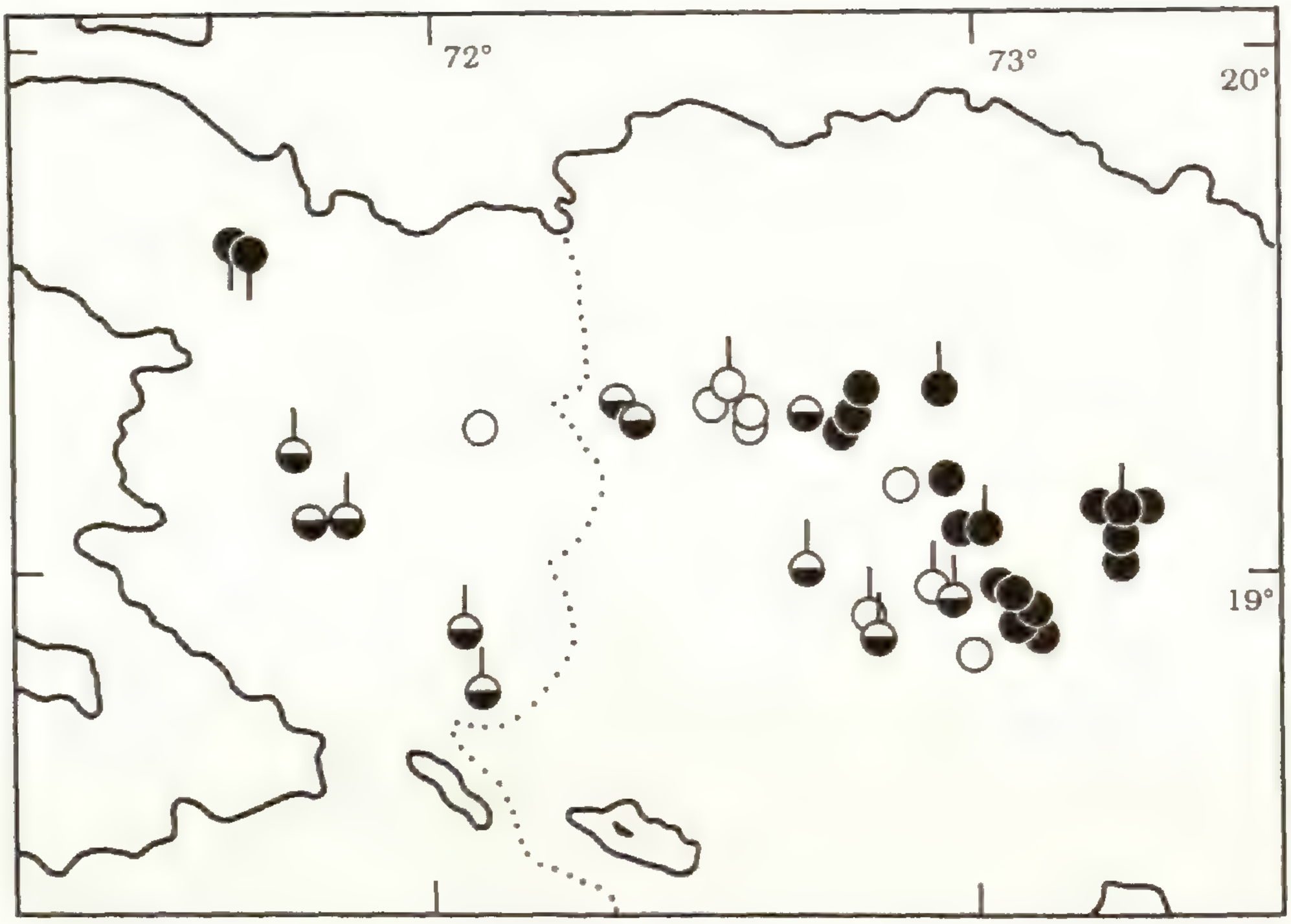



Figure 2. Geographical distribution of certain morphological features in *Miconia stenobotrys*. Dots = leaves serrate/serrulate nearly entire length, circles = leaves ± entire, half-closed circles = intermediates; tail up = stems ± flanged, no tail up = stems lacking flanges; tail down = marginal teeth associated with multicellular long-stalked hairs, no tail down = marginal teeth not associated with long-stalked hairs (or teeth lacking).

quite broadly distributed within the species' geographical range, although some are more common in a particular geographic region than another; see discussion below (and Figure 2). It is clear that different character states show independent geographical trends. In contrast, *M. stenobotrys* is easily distinguished from presumably related species (see *Phylogenetic studies* section). Thus the members of the *Miconia stenobotrys* complex are all referable to a single species, under either the phenetic or traditional-taxonomic species concepts. That is, *Miconia stenobotrys* is a morphological entity that shows no major internal discontinuities in its pattern of variation, and is separated from other such entities by a consistent morphological gap (*see* Judd, 1981, 1986; Judd and Beaman, 1988).

In contrast to many members of *Miconia* sect. *Chaenopleura*, *M. stenobotrys* has been well collected; populations from the Constanza–Jarabacoa region are especially well represented in herbaria (see Figure 1). It is clear, however, that recent collecting has

expanded our understand of this species' pattern of variation, e.g., specimens collected by Judd in the Parque Nacional José del Carmen Ramírez–El Frío region (Figure 1, circles) and in the Constanza-Jarabacoa region (Figure 1, triangles). Additional collections are needed from the Río Maguá and Loma la Vieja regions (Figure 1, groups 5 and 6).

## PHYLOGENETIC STUDIES

*Miconia stenobotrys* has more or less glabrescent leaves, stems, inflorescence axes, and hypanthia, i.e., they do not have a conspicuous indumentum of ferrugineous stellate-branched hairs found in most Antillean members of *Miconia* sect. *Chaenopleura.* Other glabrescent species include *M. barkeri* Urban & E. Ekman, *M. calycina* Cogn., *M. krugii* Cogn., *M. leptantha* Urban & E. Ekman, *M. samanensis* Urban, and *M. zanonii* Judd, Skean, & Beaman (all of Hispaniola), and these species may constitute a monophyletic group if the glabrescent condition is taken as synapomorphic. (The phylogenetic relationships of these species will be considered in more detail in a planned cladistic analysis of the Antillean species of section *Chaenopleura.*) *Miconia stenobotrys* is distinguished from the above listed glabrescent species (and from any other Antillean member of the section) by its V-folded and usually strongly falcate leaf blades and distinctive elongated inflorescences, i.e., 4.5–31.5 cm long, 2–5 cm wide, with 3 to 13 major branch-pairs (each of which is a ± raceme-like cyme). Among the populations of *M. stenobotrys* these similarities are certainly synapomorphic, and the species is, therefore, tentatively considered to be monophyletic, i.e., a cladospecies (Donoghue, 1985; Mishler, 1985; Mishler and Brandon, 1987; de Queiroz and Donoghue, 1988).

No population or group of populations within the *Miconia stenobotrys* complex can be segregated as distinct species because none are diagnosable, i.e., no population possesses a fixed character that distinguishes it from all individuals belonging to other populations. All populations of *M. stenobotrys,* in contrast, are clearly diagnosable from populations of related species, e.g., *M. krugii, M. samanensis, M. zanonii,* by fixed character differences. Thus, *Miconia stenobotrys* also constitutes a phylogenetic species in the sense of Cracraft (1989), Nixon and Wheeler (1990, p. 218), and Davis and Nixon (1992, p. 427): "the smallest aggregation

of populations . . . diagnosable by a unique combination of character states in comparable individuals."

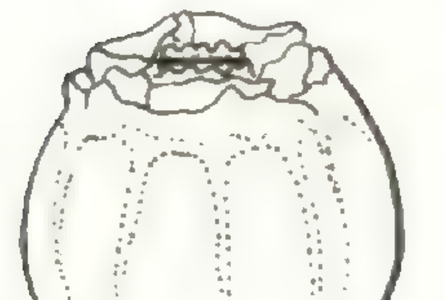
The geographical pattern of variation among populations of *Miconia stenobotrys* is outlined below. The populations in the northwestern portion of the Cordillera Central (Dominican Republic), especially in those in the vicinity of Jarabacoa, Constanza, and El Rubio, show a high frequency of individuals with strongly toothed leaves (Figure 2). Some individuals have a very slight development of stem-flanges, although most lack such structures or have them restricted to the primary inflorescence axis. Plants with leaf blades having strongly suprabasal secondary veins are more frequent in these populations than in those further east in the Cordillera Central or in the mountains of Haiti.

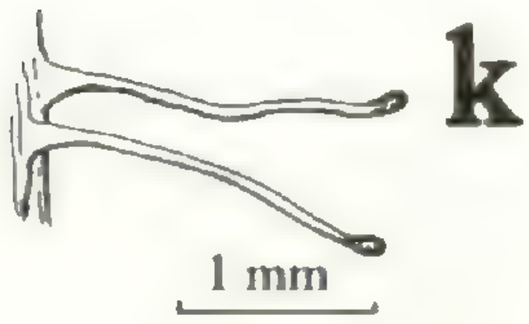
Populations of the Lagunas de Cenobí–La Cidra–La Leonor region (Cordillera Central, Dominican Republic) and the area northeast of Hinche (Massif du Nord, Haiti) are distinctive because of their entire margined leaves with the secondary veins placed very near the lamina margin (Figure 2). Occasional plants with flanged stems occur in these regions. Populations in the vicinity of Loma la Vega and the "Forestry House" (near El Frío) at the Parque Nacional José del Carmen Ramírez (Cordillera Central, Dominican Republic) are very similar to those of the La Cedra, La Leonor, and Hinche populations, but show a much stronger and consistent development of stem-flanges (Figures 2 and 3). Interestingly, the nearby and morphologically similar population near Las Lagunas (to the south of Loma la Vieja) lacks stem flanges.

Plants of the Restauración–Río Artibonito region (Cordillera Central, Dominican Republic) and populations to the west in Haiti (Figure 2) are slightly serrulate and show a variable development of stem flanges. Plants of the Río Maguá region (Cordillera Central, Dominican Republic) show variation in degree of marginal toothing and inflorescence length. These plants are thus somewhat intermediate between the three groups of populations discussed above (Figures 1 and 2).

→

Figure 3. *Miconia stenobotrys*: a, habit; b, c, leaves; d, leaf margin; e, flower; f, petal; g, berries; h, stem, showing U-shaped flanges; i, stem, lacking flanges; j, stem, x-section; k, multicellular, long-stalked, gland-headed hairs, on stem.


3 mm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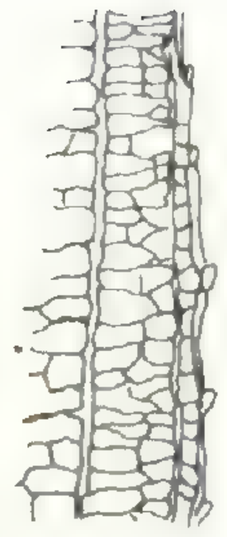
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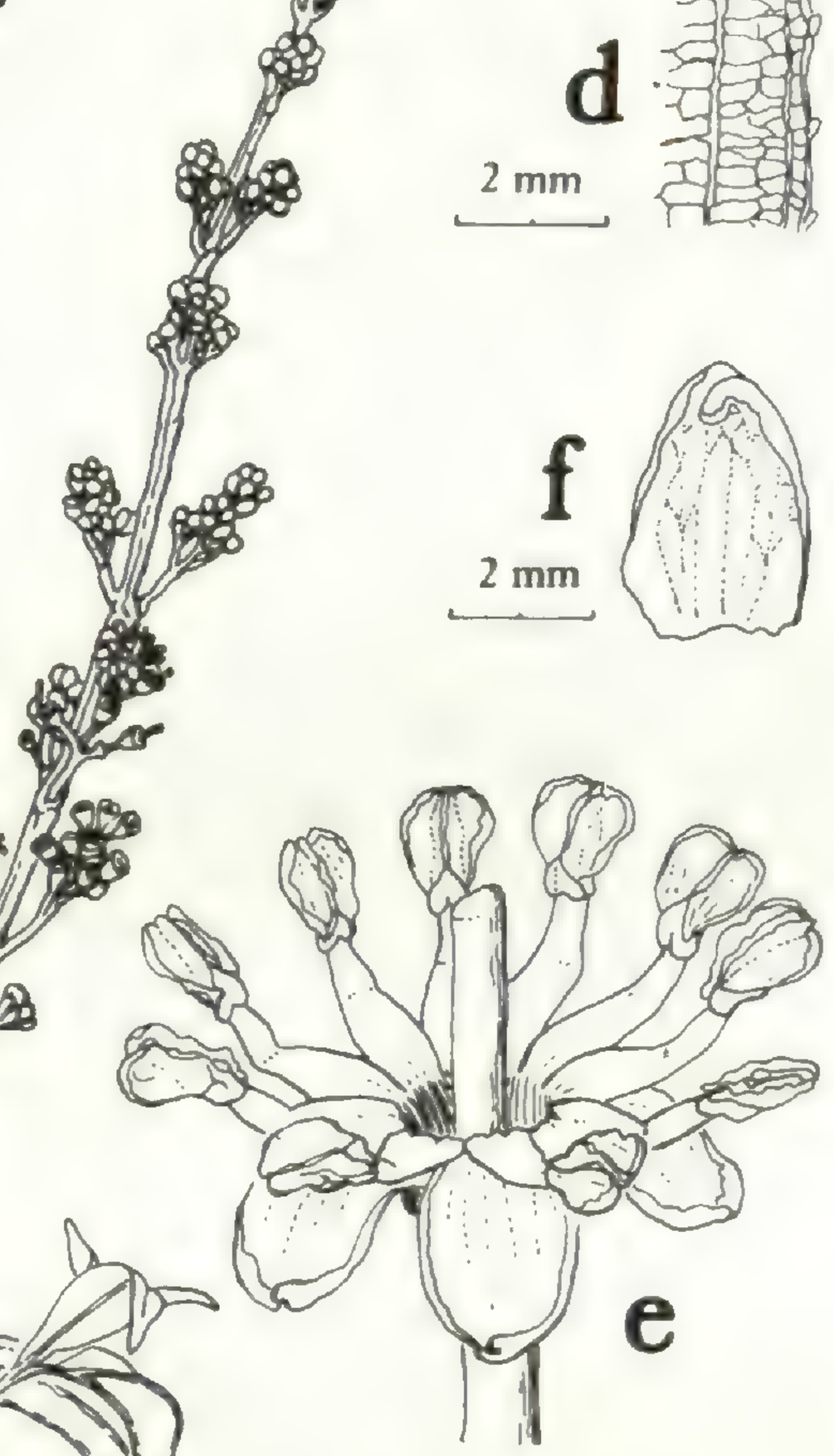
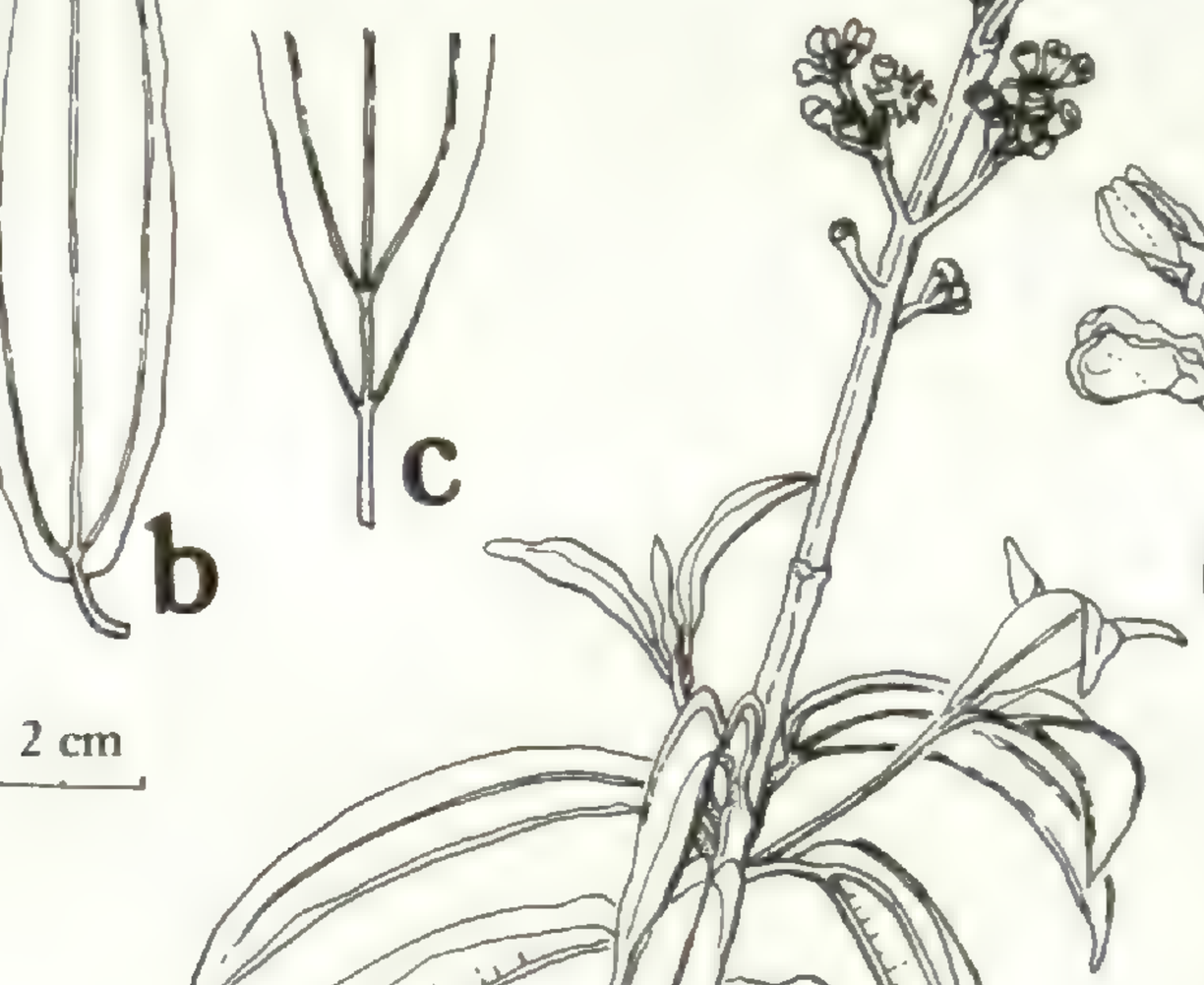
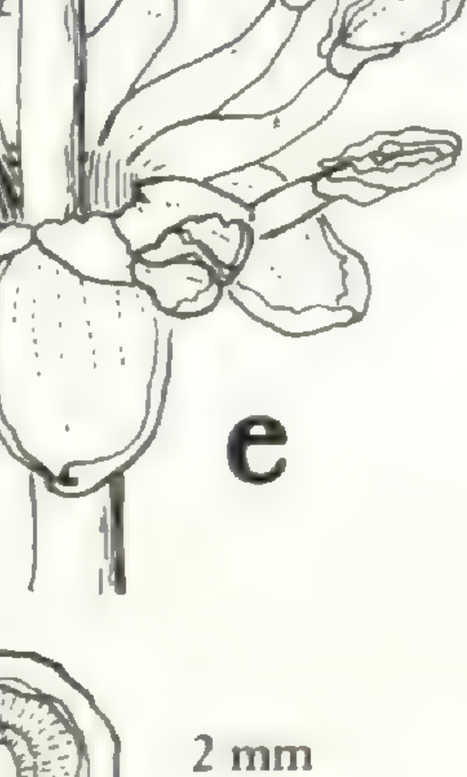

e


2 cm


a


j
2 mm

h
0.5 cm


i
0.5 cm

The plants of the Morne Belance region (Massif du Nord, Haiti) are distinguished in that their leaves are strongly serrate with a long-stalked, gland-headed hair at the apex of each tooth. Plants of other populations usually lack such hairs on their teeth. Juvenile leaves or leaves of rapidly growing shoots, however, usually possess such hairs, even in populations in which reproductive-shoot leaves are more or less entire. A similar pattern of variation, i.e., long-stalked, gland-headed hairs on teeth of juvenile leaves, is seen in several other species of section *Chaenopleura,* e.g., *M. adenocalyx* Urban & E. Ekman, *M. ferruginea* (Desr.) DC., *M. krugii, M. samanensis, M. santanana* Judd & Skean (ined.). This condition, therefore, is not used as the basis for segregating the Morne Belance plants (as *M. buchii*). Long-stalked, gland-headed hairs are also moderately scattered on stems and leaves of these plants. These hairs, however, are also found on stems (and less commonly leaves) of some plants in the remaining populations of *M. stenobotrys.* In fact, the density of gland-headed hairs is often quite variable, even within a single population. It is noteworthy that in the strongly flanged plants of the Loma La Vieja–El Frío region these hairs are usually lacking.

In summary, although certain plants of particular populations are quite different in appearance from some plants of other populations, when the total pattern of variation is considered, no diagnosable units within *Miconia stenobotrys* are discernable (Figures 1 and 2).

## TAXONOMIC TREATMENT

**Miconia stenobotrys** (L. C. Rich.) Naud., Ann. Sc. Nat., 3 ser., 16: 240. 1851.

*Melastoma stenobotrys* L. C. Rich. in Bonpl. Mélast. 66, t. 30. 1816. *Chaenopleura stenobotrys* (L. C. Rich.) DC., Prodr. 3: 197. 1828. *Miconia stenobotrys* (L. C. Rich.) Naud., Ann. Sc. Nat. 3 sér. 16: 240. 1851. TYPE: "montibus insulae Hispaniolae," *L. C. Richard s.n.*, P, not seen.

*Miconia buchii* Cogn. in Urban, Symb. antill. 5: 448. 1908. TYPE: HAITI. Dept. de L'Artibonite, Massif du Nord, Gros-Morne, Morne Belance, 1100 m, 26 Sept. 1925, *E. L. Ekman H4914* (HOLOTYPE: S!; ISOTYPE: US!).

*Miconia artibonitensis* Urban & E. Ekman, Arkiv Bot. 22A(17): 43. 1929. TYPE: DOMINICAN REPUBLIC. Prov. Monte Criste [Dajabon], Cordillera Central, near Las Rosas by Rio Artibonite, 500 m, 6 June 1926, *E. L. Ekman H6275* (HOLOTYPE: S!; ISOTYPES: IJ!, NY!, S!, US!).

*Miconia leptoneura* Urban & E. Ekman, Arkiv Bot. 22A(17): 49. 1929. TYPE:

HAITI. Dept. de L'Artibonite, Massif du Nord, near Hinche, between Cerca-Carvajal and Bois-Charles, 700 m, 12 May 1926, *E. L. Ekman H6075* (HOLOTYPE: S!; ISOTYPES: NY!, S!, US!).

*Miconia azuensis* Urban & E. Ekman, Arkiv Bot. 22A(17): 50. 1929. TYPE: DOMINICAN REPUBLIC. Prov. Azua, Cordillera Central, near Las Lagunas, 750 m, 13 June 1926, *E. L. Ekman H6374* (HOLOTYPE: S!).

*Shrub* or small *tree* to ca. 4 m tall. *Indumentum* of multicellular, minute, globular to matted and ± irregularly branched hairs, these usually ephemeral and all parts of plant glabrescent, sometimes long-stalked, gland-headed hairs to 1.9 mm long (rarely elongate, stout-stalked, shortly branched hairs). *Young twigs* rectangular to square in cross-section, 2–5 mm wide, non-ridged with a nodal line, or with 4 flanges .2–2.3 mm broad, 2 extending below each point of petiole attachment and joining to form a very obscure to conspicuous U-shaped flange at the adjacent lower node, these sometimes restricted to inflorescence axis, glabrous, or with very sparse, minute, globular to matted and ± irregularly branched hairs, these ephemeral, sometimes also with very sparse to sparse, long-stalked, gland-headed hairs, especially on portion of internode just above node (rarely with sparse, elongate, stout-stalked, shortly branched hairs); internodes .5–4.5(–9) cm long. *Leaves* with petiole 2–24 mm long, the indumentum sparse, minute, globular to matted and branched hairs, quickly glabrescent, occasionally with very sparse, long-stalked, gland-headed hairs (or rarely elongate, stout-stalked, shortly branched hairs); blade ovate to oblong (elliptic), 2.5–15.7 × .8–3.7 cm, slightly to strongly V-folded and falcate, coriaceous, the apex acuminate, the base acute to rounded (slightly cordate), the margin entire, serrulate only near tip, or serrulate/serrate to near base, ca. 5–100% of margin entire, the largest teeth (if present) .1–.6 mm long, plane to slightly revolute, especially near base, often with long-stalked, gland-headed hairs along margin at apex of teeth in juvenile shoots (occasionally in flowering shoots as well); venation acrodromous, suprabasal to nearly basal, with prominent midvein and 4 (or 2) secondary veins, with 2 conspicuous secondary veins placed ca. .7–6 mm in from margin, and usually 2 inconspicuous secondary veins closer to margin, and numerous percurrent tertiary veins oriented subperpendicular to midvein, the tertiary veins usually separated by composite inter-tertiary veins, especially proximally, the higher order veins orthogonal-reticulate; adaxial surface usually greenish (rarely slightly yellow) when dry, ± glabrous, but

initially with sparse, minute, globular hairs to matted, ± irregularly branched hairs, these quickly caducous, the midvein impressed, major secondary veins slightly impressed to flat, minor secondary and higher order veins flat, the surface appearing wrinkled after drying when druse crystals sparse (or ± papillose due to presence of numerous druse crystals just beneath surface); abaxial surface light green to red tinged, sparsely covered with minute, globular hairs and inconspicuous, matted, ± irregularly branched hairs, these usually quickly caducous, occasionally with a few long-stalked, gland-headed hairs on midvein and major secondary veins, occasionally also with very few ferrugineous, elongate and irregularly branched hairs in axils of secondary veins with midvein, ± glabrescent, the midvein prominently raised, the 2 major secondary veins slightly raised or flat, minor secondary and higher order veins flat, junctions of major secondary veins and midvein usually with pouch-like mite-domata. *Inflorescences* terminal, paniculate to extremely elongate cymes of 3 to 13 major branch-pairs (each of which is ± a raceme-like cyme), 4.5–31.5 cm long, 2–5 cm across; proximal segment of lowermost inflorescence branches .4–2 cm long, distal internodes of inflorescence branches increasingly shorter, ultimate branches .5–7 mm long, glabrous or with very sparse, minute, globular hairs (occasionally with sparse, long-stalked, gland-headed hairs); peduncle 1.4–5 cm, with similar indumentum; each inflorescence branch associated with a caducous, ovate, elliptic, to linear bract, ca. 4–35 × 1–8 mm, the apices acuminate to acute (rounded), the lowermost pair sometimes expanded and intergrading with leaves; flowers in dichasia, each subtended by 2 caducous, obovate bracteoles, ca. 3–8 × 1.3–4 mm, glabrous or with indumentum of sparse, minute globular hairs, but with fringe of minute, unbranched to poorly branched hairs along margin, their apices rounded and hooded. *Flowers* with pedicel .3–1 mm long. *Hypanthium* cylindrical, free portion 1.1–1.7 mm long, the outer surface glabrous or very sparsely covered with minute, globular or ± matted hairs, the inner surface glabrous and slightly ridged, the apices of the ridges not extending beyond rim or forming minute projections .05–.1 mm long. *External calyx lobes* (teeth) 5 (4), .05–.7 × 1.4–2.4 mm, broadly triangular to ± flat, with acute to acuminate apex, glabrous, sometimes with 1 to 3 long-stalked, hair-like projections .2–.5 mm long at or near apex of each lobe; *internal calyx lobes* 5 (4), .5–2 × 1.5–2.6 mm, broadly ovate to ovate-triangular, pale green to red, ± glabrous, the apex

rounded (acute), the margin entire to minutely erose, calyx tube .2–.5 mm. *Petals* 5 (4), broadly ovate or elliptic to orbicular, 2.8–4.5(–5.5) × 2.2–3.6 mm, glabrous, white (to red-tinged abaxially), imbricate and apically interlocking in bud, with the apex rounded, with an asymmetrically located notch. *Stamens* 10 (8), geniculate, glabrous; proximal segment (filament) 1.7–2.6 mm long, distal segment (anther and connective) 2.4–3.1 mm long, with minute dorsal projection, the anther 1.7–2.1 mm long, with fertile portion of anther sacs 1.4–1.7 mm long, opening by 2 longitudinal slit-like pores, the connective extended .6–1.2 mm beyond the base of the anther sacs. *Ovary* (2- or) 3- (or 4-) loculate ($n$ = 1, 36, 3), ca. ⅔- to ¾-inferior, ovoid, short ovoid, or subglobose, 2–2.8 × 2–3 mm, glabrous and ridged, with fluted apical projection ca. .1–.6 mm long encircling base of style; style 3–6.7 mm long. *Berries* globose to subglobose, 5–6.5 × 5–7 mm, pale gray-blue, but red when immature, ± glabrous. Seeds angular-obovoid, .7–1.3 mm long; testa smooth to minutely roughened due to slight bulging of individual cells. $2n$ = 34 (Solt and Wurdack, 1980; based on *Wurdack 2591* (NY), from seeds from *Liogier 11575* (see below)).

ETYMOLOGY: The specific epithet refers to the species' narrow and extremely elongated cymose inflorescences. The major branch pairs, numbering as many as 13, are typically well separated from each other. *Miconia stenobotrys* has longer cymes than any other species of *Miconia* sect. *Chaenopleura* in the Greater Antilles; they vary from 4.5 to 31.5 cm long and 2 to 5 cm wide.

SPECIMENS EXAMINED: HAITI. **Dept. de L'Artibonite**: Massif du Nord, La Brande [Branle] to Mt. Balance [Belance], 1065 m, *Nash & Taylor 1713* (NY). **Dept. de L'Ouest**: Massif des Cahos [= Massif Montagnes Noires], Petite-Rivière de l'Artibonite, Médor, 800 m, *Ekman H3396* (GH, IJ, S, US); Massif des Cahos, group Las Caobas [= Lascahobas], Mirebalais, Calumette, ca. 900 m, *Ekman H5567* (NY, S); Massif des Matheux [actually from Montagnes Trou D'Eau], Grand-Bois, Cornillon, 1200 m, *Ekman H5687* (A, S); near Perodin, 1200 m, *Picarda 1636* (GH, L, S). DOMINICAN REPUBLIC. **Prov. Azua**: Cordillera Central, San Juan, Loma la Vieja, southeastern spur, 1300 m, *Ekman H13410* (A, GH, NY, S, US); Loma la Vieja, in thickets, 800 m, *Ekman H13441* (GH, S). **Prov. La Vega**: Cordillera Central, Jarabacoa, Salto del Jimenoa, *Augusto 214*(JBSD); Constanza, 1200 m, *Ekman H14085* (S); near Jarabacoa, 560 m, *Fuertes 1636* (A, BM, E, F, GH, L, NY, US); without specific locality, *Fuertes 1821b* (A, E, NY); Gajo de Constanza, 1200 m, *Jiménez 2115* (IJ, US); between Constanza and Jarabacoa, ca. 23 km N of El Río, 760 m, *Judd 2955* (FLAS, JBSD, MSC, NY); ca. 20 km N of El Río on rd. to Jarabacoa, 860 m, *Judd 2958* (FLAS, US); ridge behind Hotel Nueva Suiza, 1200–1380 m, *Judd 5125* (DUKE, F, FLAS, GH, JBSD, MO, MSC, NY, S, US); ca. 21 km N of

El Río on rd. to Jarabacoa, 760 m, *Judd 5143* (FLAS, MO, MSC); 7.4 km SE of Jarabacoa, 810 m, *Judd 6626* (DUKE, F, FLAS, JBSD, MO, NY, S, US); 6.7 km SE of Jarabacoa, 720 m, *Judd 6627* (F, FLAS, MO); 6.1 km SE of Jarabacoa, 700 m, *Judd 6629* (FLAS); just S of Constanza on rd. to Valle Nuevo, 1375 m, *Judd 6653* (FLAS, MSC, S); Constanza, at Salto de Constanza, 1050 m, *Judd 6654* (FLAS, NY); ridge behind Hotel Nueva Suiza, along Río Grande, 1100–1250 m, *Judd 6659* (FLAS); La Ciénaga de Manabao, Los Guanos, Jarabacoa, *Liogier 12043* (NY, US); Río Grande, Constanza, 1250 m, *Liogier 19505* (JBSD, NY, US); near Manabao, Jarabacoa, 1000 m, *Liogier 20038* (JBSD, NY); La Ciénaga de Manabao, Jarabacoa, 1000 m, *Liogier 23584* (JBSD); 15–20 km N of El Río on rd. to Jarabacoa, 1000 m, *Mejía 7494* (FLAS, JBSD); El Pino de Siete Hojas, at La Cuenca de Yaquecillo, 16 km NW of Constanza, 1100 m, *Mejía 8833* (JBSD); 12 km NW of Constanza on rd. to Los Corralitos, near Los Cayetanos, 1000 m, *Mejía 8858* (FLAS, JBSD); 2.5 km SE of Constanza, 1250 m, *Proctor 39060* (IJ, JBSD); Constanza, along Río Grande, 1.5 km SW of Nueva Suiza Hotel, 1125 m, *Sauleda 7516* (JBSD, UPR); S of (behind) Hotel Nueva Suiza, 1200–1380 m, *Skean 1748* (FLAS, JBSD, MICH); rd. between Jarabacoa and Paso Bajito, 7.4 km S of Jarabacoa, 810 m, *Skean 3220* (FLAS, JBSD, MICH); just S of Constanza on rd. to Valle Nuevo, 1375 m, *Skean 3246* (FLAS, JBSD, MICH); near Constanza, 1200 m, *Tuerckheim 3191* (BM, E, F, GH, L, M, MO, NY, S, US); Constanza to Valle Nuevo, *Woodbury s.n.*, 6 April 1971 (UPR); 4 km SE of Constanza on road to Las Auyamas, in valley of the Río Grande, 1300 m, *Zanoni 23181* (FLAS, JBSD, US). **Prov. San Juan**: Cordillera Central, Piedra del Aguacate to Río del Oro, *Howard 9433A* (NY); Parque Nacional José del Carmen Ramírez, 14 km N of Arroyo Cano, near Los Fríos, 400 m E of the "caseta de la Dirección Nacional de Parques," 1380 m, *García 1245* (FLAS, JBSD); Parque Nacional José del Carmen Ramírez, on trail between "Forestry House" (Caseta del Forestal) to Arroyo Palo de Cuello; above Los Fríos, on the jeep road from Arroyo Cano, 1300–1400 m, *Judd 6693* (A, FLAS, JBSD, MO, NY, US); ibid., *Judd 6694* (FLAS, JBSD, NY, US); near Los Fríos, along "jeep road" from Arroyo Cano, just below (S of) "Forestry House" in Parque Nacional José del Carmen Ramírez, 1250 m, *Judd 6698* (DUKE, F, FLAS, GH, JBSD, MO, MSC, NY, S, UC, US); ibid., *Skean 3269* (FLAS, JBSD, MICH). **Prov. Santiago**: Cordillera Central, moist ravine on outskirts of San José de las Matas, 760 m, *Burch & Jiménez 2476* (US); El Rubio, Arroyo Bonito, *Canela s.n.*, 16 Nov. 1940 (JBSD); Puente Aguas Caliente, Cuenca de Rio Bao, *Hernández 11* (JBSD); ibid., *Hernández 4-3/3* (JBSD); Pico del Rubios, 1000 m, *Jiménez 1068* (US); El Rubio Peak, 800–940 m, *Liogier 11260* (NY, US); Arroyo Antonzape Malo, Mata Grande, *Liogier 11575* (NY); San José de las Matas, Punta Loma on Río Maguá, 800 m, *Valeur 736* (A, BM, F, IJ, MICH, MO, NY, S, US). **Prov. Santiago Rodriguez**: Cordillera Central, Moncíon, Lagunas de Cenoví, 1100 m, *Ekman H12870* (A, GH, S, US); La Cidra, Monción, 1000 m, *Jiménez 1616* (US); ibid., 640 m, *Jiménez 2910* (US); El Aguacate, La Leonor, Monción, 600 m, *Liogier 13218* (GH, NY, US); La Lomita, La Leonor, Monción, 550 m, *Liogier 16342* (NY, US); Sabaneta, Lagunas de Cenobí, *Valeur 17* (A, S, US); Lagunas de Cenoví, ca. 3.5 hr. by mule S of El Aguacate (de Monción), 1050–1100 m, *Zanoni 43778* (FLAS, JBSD).

DISTRIBUTION AND ECOLOGY: *Miconia stenobotrys* occurs from 550 to 1400 m elev. in moist forests of *Pinus occidentalis* Sw. (and less commonly broad-leaved thickets) of the Cordillera

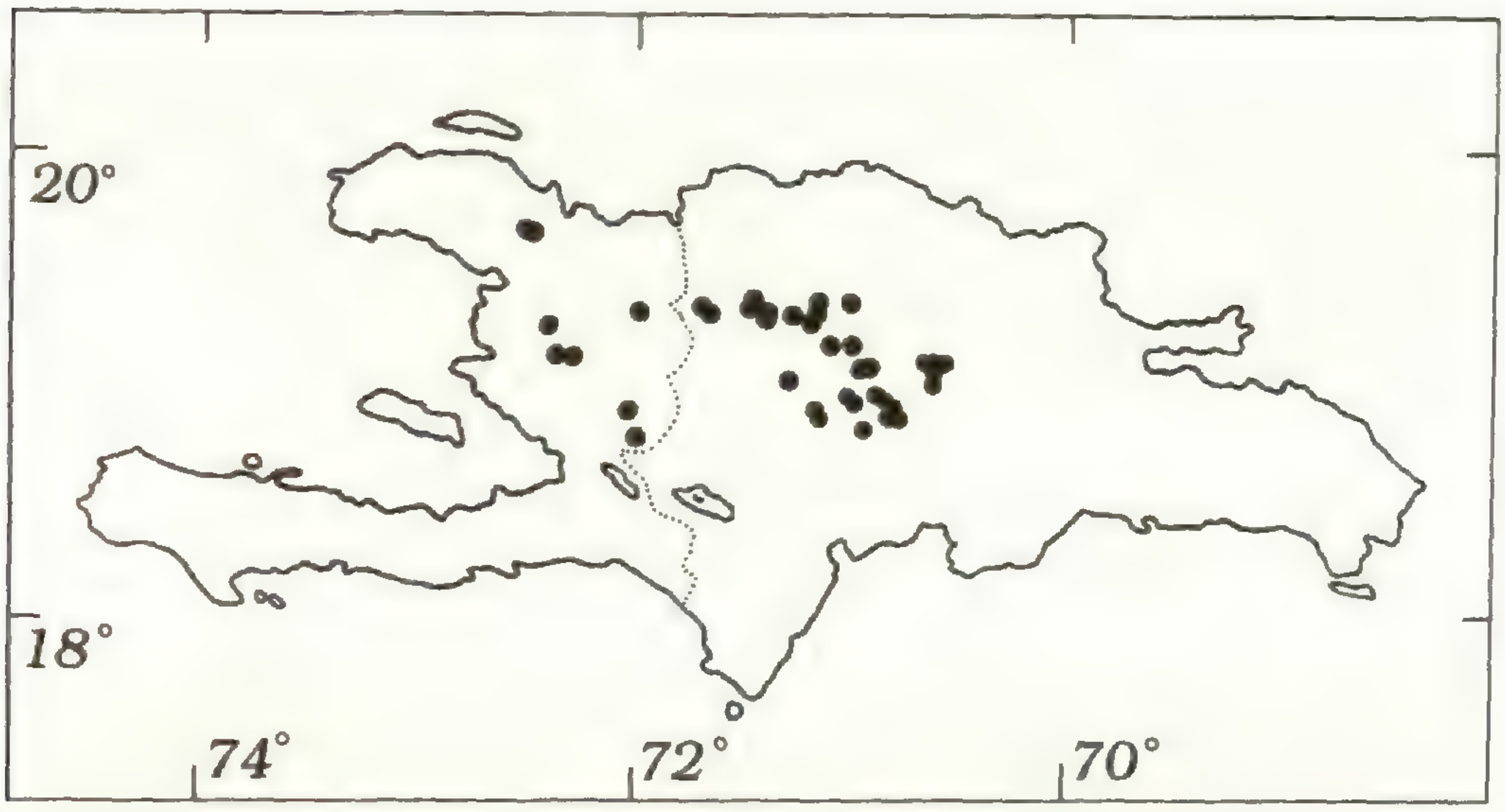



Figure 4. Distribution of *Miconia stenobotrys* (Hispaniola).

Central/Massif du Nord (Dominican Republic/Haiti), Massif Montagnes Noires/Massif des Cahos (Haiti), and Montagnes Trou D'Eau (Haiti); Figure 4. Associated melastomes include: *Calycogonium reticulatum* (Cogn.) Judd & Skean, *Calycogonium* spp., *Clidemia angustilamina* Judd & Skean, *C. hirta* (L.) D. Don, *C. umbellata* (Mill.) L. O. Williams, *Mecranium acuminatum* (DC.) Skean, *M. puberulum* Cogn., *Meriania involucrata* (Desr.) Naud., *Miconia adenocalyx* Urban & E. Ekman, *M. laevigata* (L.) DC., *M. mirabilis* (Aubl.) L. O. Williams, *M. prasina* (Sw.) DC., *M. santanana* Judd & Skean (ined.), *M. tetrandra* (Sw.) DC., *Ossaea* [*Sagraea*] *scalpta* (Vent.) DC., *Tetrazygia crotonifolia* (Desr.) DC., *T. longicollis* Urban & Cogn., and *Tibouchina longifolia* (Vahl) Baill.

*Miconia stenobotrys* is one of the most widely distributed of the Hispaniolan members of *Miconia* sect. *Chaenopleura.* It is elevationally and/or geographically isolated from the possibly related *M. krugii, M. samanensis,* and *M. zanonii* (see also Judd & Beaman, 1988). It has been collected in the vicinity of only two species of sect. *Chaenopleura,* both members of the *Miconia ferruginea* complex, i.e., *M. adenocalyx* and *M. santanana* (ined.) (Judd & Skean, submitted). These species, however, typically grow in moist cloud forests or moist broadleaved forests along streams, while *M. stenobotrys* is characteristic of pineland habitats, and are likely isolated ecologically. An unusual specimen (*Ekman 12895,* s) is intermediate between *M. stenobotrys* and *M. santan-*

*ana* and may represent a hybrid between these two sympatric species. This specimen is aberrant in its broadly branched cymes (with cymose-branched lower branches), stems inflorescence axes with numerous long-stalked gland-headed hairs and persistent, ferrugineous, stellate-branched hairs, and ± non-falcate leaves with tertiary veins slightly abaxially raised.

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# A NEW RECORD FOR *TILLANDSIA* (BROMELIACEAE) IN FLORIDA

HARRY E. LUTHER

**ABSTRACT**

*Tillandsia fasciculata* var. *fasciculata* is recorded for the first time in Florida. It may be distinguished from the common *T. fasciculata* var. *densispica* by longer inflorescence branches and larger floral bracts.

Key Words: Bromeliaceae Florida Systematics *Tillandsia*

*Tillandsia fasciculata* Swartz is one of the most colorful and conspicuous epiphytes in peninsular Florida. While it is most numerous in the Everglades and Big Cypress regions of southern Florida, diffuse populations extend northward into Citrus and Flagler counties. Reports from Georgia (Brooks, 1968) have not been confirmed (Callison, 1992). The latest monograph of the Bromeliaceae (Smith and Downs, 1977) accepts ten varieties of *T. fasciculata*. More recently, several of these have been elevated to specific rank (Gardner, 1984), or are considered to be of hybrid origin (Luther, 1985). The remaining taxa can be conveniently divided into two groups based on the length of the fertile portion of the inflorescence branches (more than or less than 10 cm) and the length of the floral bracts (20–30 mm or 35–50 mm long) (Smith and Downs, 1977).

The majority of the *Tillandsia fasciculata* plants in Florida belong to var. *densispica* Mez (Figure 1). This variety, based on a type collected at Merritt Island in Broward county, Florida (*Curtiss 2844*, K, GH, US!), is characterized by a digitate or densely pinnate inflorescence of subsessile or short-stipitate branches with floral bracts 20–30 (mostly 22–25) mm long. The inflorescence is generally bright colored with red, red and yellow, or orange bracts and blue-violet petals. Rarely, a plant with green bracts and white petals (forma *alba* M. B. Foster) is encountered. Many thousands of plants of *T. fasciculata* var. *densispica* have been transplanted into gardens throughout the warmer portions of the state.

Very uncommon are individuals of *Tillandsia fasciculata* var. *clavispica* Mez. This variety, based on a Cuban type (*Eggers 4730*, K, P, US!), is distinguished from the very similar var. *densispica* by a generally laxer and more ample inflorescence with clavate branches, each with a long, slender, bracteate sterile base. The

Figure 1. *T. fasciculata* var. *densispica,* a somewhat etiolated specimen from coastal Sarasota County.

Figure 2. *T. fasciculata* var. *fasciculata,* from southern Dade County.

floral dimensions are essentially the same in var. *densispica.* Superficially "pure" examples are rare in southern Florida and several collections from Broward and Collier counties appear to represent the results of introgression with the abundant var. *densispica.* Occasional reintroduction of var. *clavispica* by airborne seeds

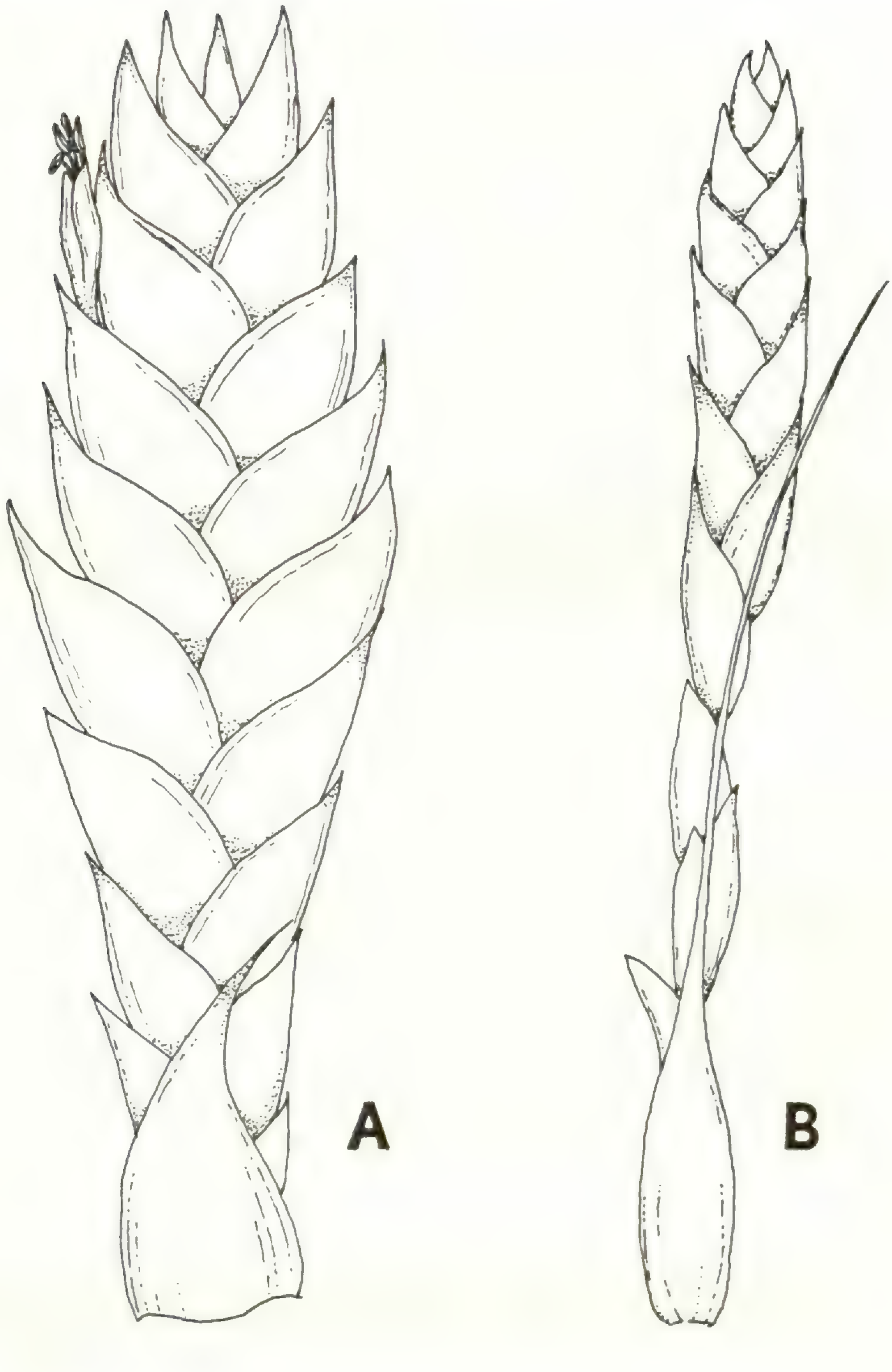


Figure 3. A. *Tillandsia fasciculata* Sw. var. *fasciculata*. U.S.A. Florida; Dade county, *Dowling s.n.* B. *Tillandsia fasciculata* Sw. var. *densispica* Mez. U.S.A. Florida; Sarasota county, *Mickler s.n.*

from Cuba appears to maintain a residual population which would otherwise be swamped through hybridization with the much more numerous plants of var. *densispica*.

Recently a cultivated specimen, originally from southern Dade county, of the larger flowered *Tillandsia fasciculata* var. *fasciculata* (Figure 2) has been brought to my attention. This variety, originally collected in Jamaica (*Swartz s.n.*, S, photo at GH!), is widespread throughout the West Indies, Mexico, and Central America to northern South America. Its occurrence in southern Florida is certainly not unexpected but, until now, not verified. For the record, the voucher for this new record for the flora of Florida is cited herewith:

> *Tillandsia fasciculata* Sw. var. *fasciculata*. USA. Florida. Dade county: vicinity of Fuchs Hammock, *C. F. Dowling s.n.* 1970. Flowered in cultivation, 14 June 1992, *M. Prince s.n.* (SEL!, FLAS!).

This variety can be distinguished from the common plants of *Tillandsia fasciculata* var. *densispica* by a more spreading rosette of dark grey green (not grey or silver) leaves and longer (40–48 mm long not 20–30 mm long) floral bracts. The coloration of the inflorescence of the Fuchs Hammock plant is atypically subdued; yellow-green, not red or red and yellow as is common in other areas.

The lack of additional, confirming collections suggests that this taxon is rare or no longer established in Florida. Perhaps the occasionally freezing weather or extended winter dry season present too rigorous conditions for its survival or spread. On the other hand, specimens may have simply been overlooked. Additional field work in Dade and Monroe counties is needed to ascertain current status and distribution of this taxon.

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# SOME UNWELCOME ADDITIONS TO THE FLORA OF NEW HAMPSHIRE

DONALD J. PADGETT AND GARRETT E. CROW

ABSTRACT

During the last decade the discovery of a number of new plant localities have added additional species to the flora of New Hampshire. Most of those have been native plants, and the new sites are valued records for the data base on rare plants. Three of the additions reported here are aggressive weeds of aquatic habitats, a fourth is an introduction of exotic germ plasm in a wetland habitat. They are less than welcome additions to the flora of the state.

Key Words: Wetlands, weeds, *Najas minor, Scirpus fluviatilis, Potamogeton crispus, Myriophyllum spicatum*

**Najas minor** All.

The Minor Naiad or Eutrophic Water-nymph is one of the more distinctive species of *Najas,* with its conspicuously serrulate leaves that become recurved with age (Haynes, 1979). This European species, first introduced into North America about 60 years ago, has continued to extend its range throughout northeastern United States (Meriläinen, 1968). New England localities are few and were reported by Hellquist and Crow (1980) from western Vermont and western Massachusetts, growing in alkaline waters.

During a study of created wetlands in southeastern New Hampshire in 1992 (Padgett and Crow, in press a and b), a population of *Najas minor* was discovered in Rockingham County. The site was a six year old created wetland, serving as mitigation for a wetland destroyed during the construction of a new hospital in Portsmouth. Since the mitigation plan involved a natural colonization of vegetation largely derived from the seed and propagule bank provided in the transportation of wetland muck from the hospital site and spread as a dressing at the mitigation site, no planting scheme was carried out at the site. While its introduction remains a bit puzzling, seeds could have been introduced by water fowl. *Najas minor* has been reported to invade recently constructed artificial lakes and ponds in Ohio (Wentz and Stuckey, 1971).

SPECIMENS: **New Hampshire.** Rockingham Co.: City of Portsmouth, H.C.A. created wetland, west side of Route 1. 22 July

1992, *D. J. Padgett 167*; 1 September 1992, *D. J. Padgett 236* (NHA).

**Scirpus fluviatilis** (Torr.) A. Gray

In another created wetland included in the study cited above, River Bulrush was discovered as a new addition to the flora of New Hampshire. The wetland site was created as mitigation for wetlands impacted by the construction of a mall in Salem. The population was established as part of a planting scheme designed by consultants responsible for the mitigation project. Acquired from a Wisconsin supplier, approximately 6000 tubers of *S. fluviatilis* were planted during the summer of 1990. This planting appears to be successful, with a population forming a very dense, fertile stand.

This new record represents a situation of some concern. While *Scirpus fluviatilis* is actually native to New England, having been reported from Maine, Vermont, Massachusetts and Connecticut, it is listed as a rare plant of "special concern" in Massachusetts (Coddington and Field, 1978; Sorrie, 1987), presently regarded as "threatened" in Connecticut, and is currently being evaluated for rareness for the New England region by the *Flora Conservanda* project, New England Conservation Program. We certainly question the ethics of deliberately introducing plants into a region where native populations are in need of conservation (Padgett and Crow, in press c).

SPECIMENS: **New Hampshire.** Rockingham Co.: Town of Salem, created wetland at southernmost entrance of The Mall at Rockingham Park, Rockingham Park Blvd. 24 August 1992, *D. J. Padgett 354* (NHA).

**Potamogeton crispus** L.

*Potamogeton crispus* (Curly Pondweed), a Eurasian plant, is a widely distributed adventive species which has become a troublesome weed in many parts of the United States (Stuckey, 1979) and is rapidly spreading in bordering Canada (Catling and Dobson, 1985). In New England it occurs primarily in scattered locations throughout western and southern portions of the region and in polluted ponds and streams in eastern Massachusetts (Hellquist and Crow, 1980). The earliest documented occurrence in

New Hampshire is a specimen collected by C. B. Hellquist from the Connecticut River, collected in 1984. That same year specimen fragments from an artificial pond in Hampton, NH, were brought in to the Hodgdon Herbarium for identification, which G. Crow determined as *P. crispus*. This occurrence in southeastern New Hampshire was not unexpected, as the species has been reported from nearby Massachusetts, growing in the Merrimack River, West Newbury (Caldwell and Crow, 1992).

SPECIMENS. **New Hampshire.** Cheshire Co.: Walpole, west shore of Connecticut River east of backwater ca. 1.5 miles north of Bellows Falls, VT. 4 September 1984, *C. B. Hellquist 15446* (NASC, NHA).

**Myriophyllum spicatum** L.

Eurasian Milfoil is an especially unwelcome addition to the flora of New Hampshire. Crow and Hellquist (1983) reported this noxious weed as locally abundant and aggressive in alkaline waters of western Vermont and Massachusetts, with only one locality in eastern Massachusetts and one in northeastern Connecticut. The first record for New Hampshire is based on a collection submitted by the New Hampshire Water Supply and Pollution Control Commission to the Hodgdon Herbarium for identification; G. E. Crow confirmed its identity as *Myriophyllum spicatum*. The plant was found to be choking the waters of Mountain Lake, Brookfield, an isolated pond whose access is by a poor road requiring 4-wheel drive. Its appearance in this remote locality with soft waters remains a puzzle. A handy field character for recognizing this species, even in vegetative condition, is that the ends of the uppermost feather-like leaves are flat-topped, as if trimmed by a pair of scissors (Crow and Hellquist, 1983, in press).

SPECIMENS: **New Hampshire.** Strafford Co.: Town of Brookfield, Mountain Lake. 3 September 1992, *K. Warren, s.n.* (NHA).

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# NOTES ON *CHAMAESYCE* (EUPHORBIACEAE) IN FLORIDA

ALAN HERNDON

## ABSTRACT

Twenty-three species of *Chamaesyce* are presently known to grow in Florida. A new key to the Florida species is presented along with notes on taxonomically important morphological characters in the genus and a review of the various names applied to each species.

Key Words: *Chamaesyce*, Florida

## INTRODUCTION

Species of *Chamaesyce* in Florida are easy to identify once learned, but the learning process is significantly impeded by the available literature. A large part of the confusion has arisen due to a change in the application of several names between 1933 and 1965. In the worst case, the name *C. maculata* is applied to two entirely different species, both very widespread and common, in regional floras frequently used to identify plants collected in Florida. More confusion is created by the specialized vocabulary used in descriptions of species from this group. Finally some of the confusion must be attributed to the continued use of some inappropriate characters in identification keys.

The major purpose of this paper is to provide a unified treatment of the Florida species. Following a discussion of some taxonomic characters of particular importance in the identification of *Chamaesyce* species, a key to the Florida species is presented. Finally, additional notes are provided on the identification of species and a guide to the previous treatment of each species in regional literature.

## GENERAL CHARACTERISTICS OF *CHAMAESYCE*

With some exceptions, species of *Chamaesyce* are small, herbaceous plants. They grow best in sunny, sparsely vegetated areas and are often conspicuous weeds where the soil surface is cleared frequently (such as gardens) or competing vegetation is held in check by frequent mechanical disturbance (especially roadsides).

Most of the species in Florida are annuals. Only a few species with West Indian affinities (restricted to southernmost Florida) are perennial. A few of the larger species occasionally develop a small woody base and one coastal species (*C. mesembryanthemifolia* is a subshrub.

Leaves are opposite (distichous), stipulate and usually have distinctly inequilateral bases. Stipules may be either united or free. Veins are surrounded by specialized sheath cells associated with C4 metabolism.

## TAXONOMICALLY IMPORTANT MORPHOLOGICAL CHARACTERS

Small (1933) used growth habit (stems erect versus stems prostrate) as one of the primary characters for distinguishing species in his treatment of the genus. Despite having recognized the limitations of habit in an unpublished dissertation (Burch, 1965), Burch (1966) retained it as an important character in his key to the species. More useful for identification is the differentiation between upper and lower stem surfaces in some pubescent species, a character independent of the habit of an individual plant. (This differentiation is found in species that commonly have prostrate growth form, so it is reasonable to speak of upper and lower surfaces.) When examining specimens, it is important to realize that prostrate growing plants are often mounted on herbarium sheets in such a way that only the lower side of the stems is visible. It may be necessary to search carefully along the sides of the stems on such specimens to find the pubescence characteristic of the upper stem surface.

Leaf shape can often be used to place specimens in small groups of species (Figure 1). The presence of serrate or dentate leaf margins is as important as overall leaf shape. In most cases, the presence of serration is clear, although it may be so only under magnification. In *Chamaesyce blodgettii,* some of the larger leaves on every specimen will have a few dentations but most leaves will have entire margins. Another leaf characteristic of some importance is thickness. Most species have a thin lamina. When such leaves are examined using transmitted light, the bundle sheaths surrounding the veins in the leaves show up as a dark reticulate network in the lamina. In the *C. deltoidea* complex and the *C. garberi* complex, however, the leaf lamina is sufficiently thick that the bundle sheaths do not contrast strongly. This is

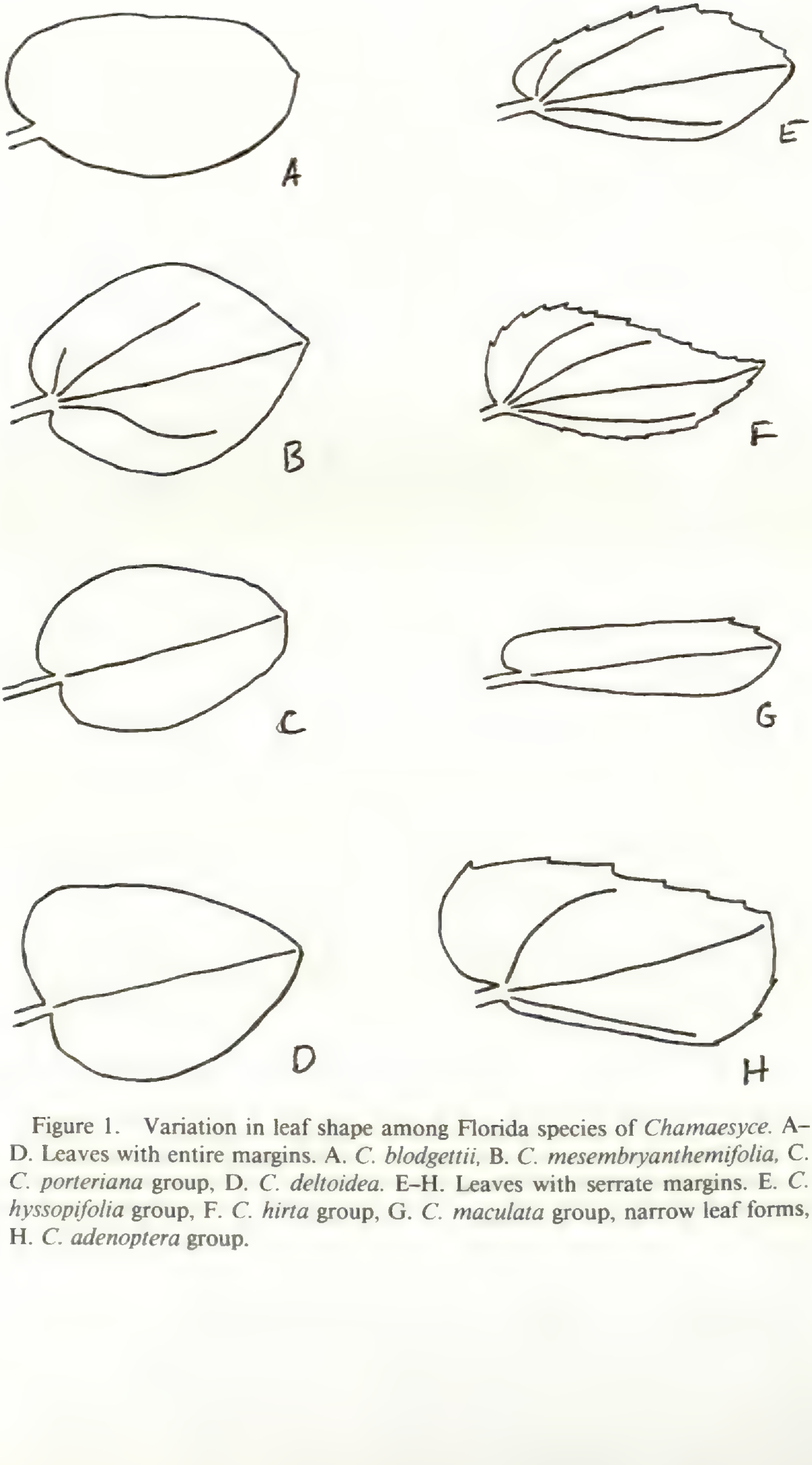


Figure 1. Variation in leaf shape among Florida species of *Chamaesyce*. A–D. Leaves with entire margins. A. *C. blodgettii*, B. *C. mesembryanthemifolia*, C. *C. porteriana* group, D. *C. deltoidea*. E–H. Leaves with serrate margins. E. *C. hyssopifolia* group, F. *C. hirta* group, G. *C. maculata* group, narrow leaf forms, H. *C. adenoptera* group.

particularly important because it provides an easy way to distinguish *C. blodgettii* from *C. porteriana.* The taxonomic importance of the presence or absence of a cyanic blotch near the center of the leaf blade has been overemphasized. In species possessing this feature, the pigmented area may be present or absent on individual plants. In other words, the absence of this coloration is not informative.

Pubescence provides particularly useful characters for the identification of species. In general, the presence or absence of pubescence on capsules and/or stems is used to separate species, although *Chamaesyce deltoidea,* as treated herein, contains both glabrous and densely pubescent populations and *C. hyssopifolia* includes glabrous and slightly pubescent individuals.

Position and arrangement of groups of cyathia is very useful for the recognition of species. There is, in fact, a continuum in arrangements from solitary cyathia in leaf axils through the production of slightly modified axillary branch systems bearing solitary axial cyathia to highly modified axillary branch systems with dichotomous or pseudo-dichotomous branching and leaves reduced to bract-like structures or completely missing. The important distinction in the key is between the dichotomously branched inflorescences and all other forms.

Glands on most Florida species are elliptic and 2–4 times as long as wide, but some groups show significant variations (Figure 2). Specimens of *Chamaesyce polygonifolia* collected in Florida show irregular gland production with individual cyathia showing variable numbers of glands. Other Florida species produce four glands on each cyathium. Appearance of the petaloid appendages of the glands can be important for the identification of specimens. In the *C. deltoidea* complex and *C. ophthalmica,* these appendages are very narrow or altogether lacking. In the *C. adenoptera* complex, the gland appendages are greatly inequal in size (Figure 2e). In other groups, the gland appendages are conspicuous, at least with a hand lens. Usually, these species show considerable variation in the size of the gland appendages.

Seed structure is more useful for defining related groups of species than for identifying specimens. Most of the Florida species of *Chamaesyce* have dark brown to white, 4-sided seeds. (Immature seeds with a golden brown color generally have the same shape and surface characteristics as mature seed.) However, three Florida species (*C. bombensis, C. cumulicola,* and *C. polygoni-*

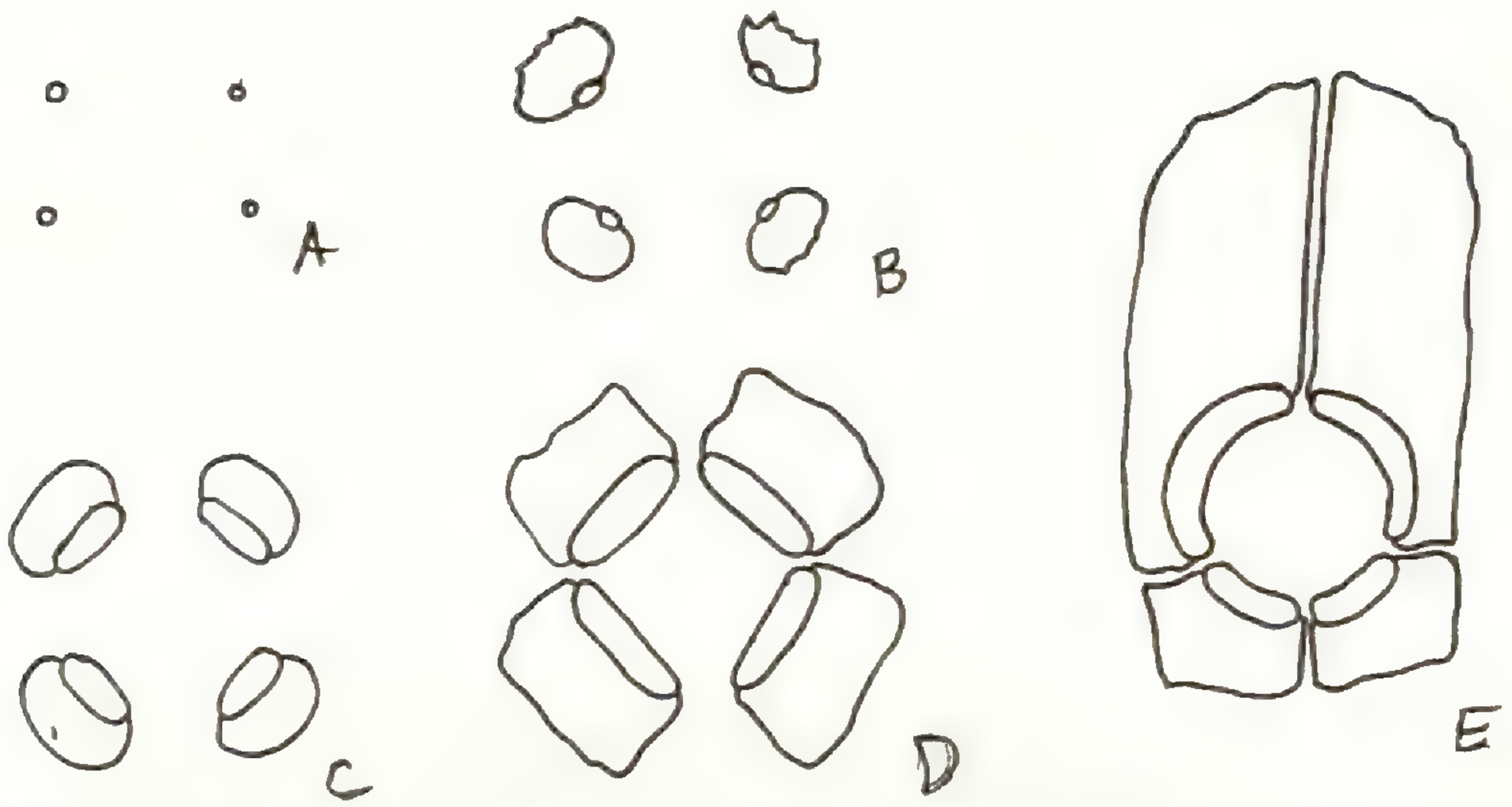


Figure 2. Variation in gland shape among Florida species of *Chamaesyce*. Gland appendages may differ greatly from those depicted. A. Minute circular glands characteristic of *C. hirta* and *C. ophthalmica,* B. Small, elliptic glands characteristic of the *C. polygonifolia* and *C. hyssopifolia* groups, C. Medium size, elliptic glands of the type found on most Florida species of *Chamaesyce,* D. Large, elliptic glands characteristic of the *C. garberi* group, and E. Unequal, lunate glands characteristic of the *C. adenoptera* group.

*folia*) have rounded seeds without flat sides that are always white at maturity.

Stipules provide useful characters for identifying species of *Chamaesyce* (Figure 3), but they must be used with caution. In most species there is considerable variation in stipule shape from plant to plant, or even from node to node on the same stem, so several stipules must be examined to determine the common shape for a given specimen. It is most important (and difficult) to determine whether the stipules are usually separated or joined. Joined stipules may be completely joined (triangular interpetiolar stipules) or nearly divided and joined only near the base (Figures 3c–3h). Joined stipules can also be torn apart by the expansion of cyathia or branches at their nodes. In some cases, the conspicuousness of the ligule is used as an identification aid. In these cases, the size of the ligule is less important than the contrast between the color of the ligule and the stem.

## SYSTEMATIC TREATMENT

**Chamaesyce** S. F. Gray, Nat. Arr. Bril. Pl. 2: 260. 1821.

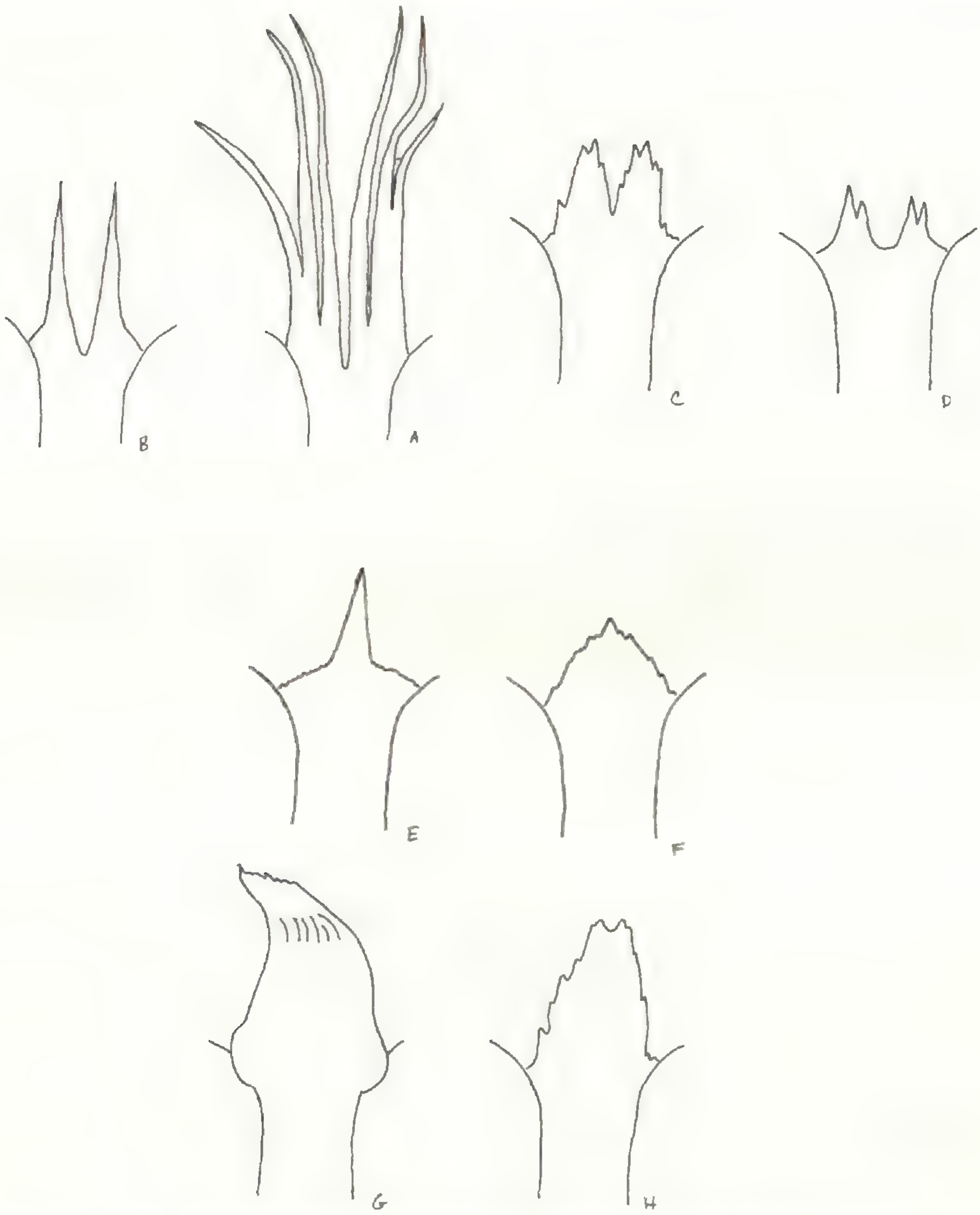


Figure 3. Variation in stipule morphology among Florida species of *Chamaesyce*. Variations in pubescence are not shown. There is often considerable variation in stipules at different nodes of the same plant. A–B. Separate stipules. A. Lacerate stipules characteristic of the *C. polygonifolia* group, B. Long acuminate stipules characteristic of the *C. hirta, C. maculata* and *C. adenoptera* groups. C–D. Stipules joined near the base only. C. *C. prostrata*, D. *C. porteriana* group. E–H. Stipules joined throughout their length. E. *C. hyssopifolia*, F. *C. mesembryanthemifolia*, G. *C. hypericifolia*, H. *C. blodgettii*.

Herbaceous, occasionally suffrutescent, annuals or perennials (one species in our area a subshrub). Trichomes, when present, simple, multicellular hairs. Leaves opposite, stipulate; the stipules either free or joined; leaf bases usually inequilateral. Inflorescence a cyathium surrounded by 4 glands (rarely fewer) or a 5th gland vestigial; petaloid gland appendages either present or absent. Fruit a trilocular capsule with each locule containing a single seed. The seed ecarunculate but with a distinct linear scar.

The following key assumes that at least immature fruits are present on the specimen.

### KEY TO THE SPECIES OF *CHAMAESYCE* IN FLORIDA

1. Capsules glabrous
   2. Cyathia in clusters or in conspicuously reduced, dichotomously branched inflorescences
      3. Plants consistently pubescent on upper part of stem and young leaves . . *C. nutans* (p. 364)
      3a. Plants glabrous throughout or with isolated stems and leaves pubescent
         4. Stipules conspicuous, 1–1.5 mm long, much longer than wide; mature capsules less than 1.3 mm long . . . . . *C. hypericifolia* (p. 364)
         4a. Stipules inconspicuous, about .5 mm long, usually not as long as wide; mature capsules more than 1.3 mm long . . . . . *C. hyssopifolia* (p. 364)
   2a. Cyathia solitary in leaf axils, terminal, or in reduced, unbranched axillary inflorescences
      5. Stipules separate, laciniate
         6. Seeds more than 2.2 mm long; cyathia evidently terminal on stems . . . . . *C. polygonifolia* (p. 365)
      6a. Seeds <1.8 mm long; cyathia either terminal or solitary in leaf axils
         7. Seeds 1.5–1.8 mm long; leaves often appearing somewhat fleshy . . . . . *C. bombensis* (p. 365)
      7a. Seeds 1.1–1.4 mm long; leaves not appearing fleshy

8. Leaves linear to narrowly elliptic, 4–5 times as long as wide, with a red margin ..... ..... *C. cumulicola* (p. 365)

8a. Leaves elliptic, less than 2 times as long as wide, concolorous ..... *C. cordifolia* (p. 365)

5a. Stipules united

9. Stipules white, conspicuous

10. Stipules about .5 mm; plants creeping herbs, often rooting at nodes

11. Calyx lobes green, less than 2 mm long, appressed to capsule. .. *C. blodgettii* (p. 361)

11a. Calyx lobes white, more than 2 mm long, free from capsule. ..... *C. serpens* (p. 367)

10a. Stipules about 1 mm; plants erect to reclining subshrubs ..... *C. mesembryanthemifolia* (p. 367)

9a. Stipules inconspicuous

12. Stems numerous from enlarged rootstock, wiry, less than 1 mm wide at base ..... *C. deltoidea* (p. 362)

12a. Stems usually 4–5 radiating from a taproot, more than 1 mm wide at base

13. Glands .5–.6 mm long, leaves thick *C. porteriana* (p. 363)

13a. Glands .2–.4 mm long, leaves thin .. *C. blodgettii* (p. 361)

1a. Capsules pubescent

14. Pubescence most abundant on the angles of the capsule

15. Gland appendages conspicuous, leaves elliptic, light green ..... *C. mendezii* (p. 366)

15a. Gland appendages inconspicuous, leaves widely elliptic, dark green .... *C. prostrata* (p. 366)

14a. Pubescence spread over the entire surface of the capsule

16. Cyathia in clusters, or in reduced, dichotomously branched axillary inflorescences

17. Gland appendages lacking, inflorescences terminal ..... *C. ophthalmica* (p. 364)
17a. Gland appendages present, sometimes small; inflorescences axial or terminal
18. Plants coarsely pubescent, trichomes on stem of two types, the larger 3–5 mm long ..... *C. hirta* (p. 363)
18a. Plants finely pubescent, trichomes to 1 mm long *C. lasiocarpa* (p. 364)
16a. Cyathia solitary in leaf axils, or in reduced, unbranched axillary inflorescences
19. Gland appendages greatly unequal in size, the larger pair at least twice as large as the smaller
20. Glands elliptic ..... *C. thymifolia* (p. 365)
20a. Glands lunate
21. Stem trichomes appressed, to .3 mm long; gland appendages white ..... *C. pergamena* (p. 361)
21a. Stem trichomes spreading, .5 mm long; gland appendages reddish *C. conferta* (p. 361)
19a. Gland appendages approximately equal in size
22. Stems pubescent on one side only
23. Adventitious roots formed at middle nodes along the stem ..... *C. humistrata* (p. 365)
23a. Adventitious roots not formed
24. Styles clavate .3–.4 mm long, seeds 1.0–1.1 mm long ..... *C. maculata* (p. 365)
24a. Styles slender, .5–.6 mm long, seeds .7–.8 mm long ..... *C. thymifolia* (p. 365)
22a. Stems pubescent on all sides
25. Stems numerous from an enlarged rootstock, less than 1

mm thick at base .....
..... *C. deltoidea* (p. 362)

25a. Stems few to several from a taproot, more than 1 mm thick at base .. *C. garberi* (p. 362)

## NOTES ON SPECIES

### *Chamaesyce blodgettii* (Engelmann ex Hitchcock) Small

Young plants of *Chamaesyce blodgettii* with large leaves and sparse branching look very similar to plants of *C. porteriana,* but are easily distinguished from that species by the small size of the glands and the more prominent stipules. Also, *C. blodgettii* specimens almost always have some (larger) leaves with dentate margins, but this character is rare on specimens of *C. porteriana.* With fresh specimens, the thickness of the leaf blade provides an easy way of distinguishing between the two species. When a leaf of *C. blodgettii* is examined by transmitted light, the network of bundle sheaths appears dark in contrast to the remainder of the lamina. If a leaf of *C. porteriana* is examined in the same way, the network of bundle sheaths are either invisible or indistinct. Heavily branched plants of *C. blodgettii* with small leaves can be confused with *C. serpens* but *C. blodgettii* has more elliptic leaves and less conspicuous stipules. When necessary, the identification can be confirmed by examination of the structure attached to the base of almost mature capsules. In *C. blodgettii,* and most other species of *Chamaesyce,* this structure is a three-lobed pad. The lobes are green, less than 2 mm long and appressed to the capsule. In *C. serpens* the lobes are white, more than 2 mm long, and free from the capsule. The general appearance of *C. blodgettii* in prostrate plants can be very similar to that of *C. maculata.* These species are easily separated by the pubescence of the latter, but this pubescence is not evident except on close examination. *C. chiogenes* Small, and *C. nashii* Small have been used for some of the more extreme forms of this species.

### *Chamaesyce dioeca* complex

*Chamaesyce conferta* Small and *C. pergamena* Small are very similar in overall appearance with curved glands, very unequal gland appendages, separate stipules with long acuminate tips and

very unequal leaf bases. Capsules are often not apparent on specimens, being hidden beneath the large pair of gland appendages; they are densely pubescent, with long appressed trichomes.

*Chamaesyce conferta* is an annual with reddish gland appendages. Compared to *C. pergamena,* it has shaggier pubescence and longer styles. Burch (1965) suggests that Florida populations should be considered conspecific with *C. dioeca,* but the Florida populations have much shorter styles than typical *C. dioeca.*

*Chamaesyce pergamena* (Small) Small is a perennial plant with a large rootstock. It is usually treated as either *Chamaesyce adenoptera* (Bertolini) Small or *C. adenoptera* (Bertolini) Small ssp. *pergamena* (Small) Burch, but the seed differences cited in Burch (1965) suggest that different species may be involved. I am retaining the name *C. pergamena* for the Florida plants pending a detailed comparison with West Indian specimens. It differs from *C. conferta* in having white gland appendages and shorter, more uniform pubescence.

*Chamaesyce deltoidea* (Engelmann ex Chapman) Small

A highly variable species with four strongly differentiated subspecies that have all been treated as separate species in the past. It is characterized by many wiry stems radiating from an enlarged woody rootstock, shallowly cordate leaf bases, and gland appendages very small to lacking. Subspecies *deltoidea* has glabrous or sparsely puberulent stems that are appressed to the substrate. Subspecies *adhaerens* has appressed to ascending stems with dense pubescence of irregularly twisted trichomes. Subspecies *pinetorum* has erect stems with a dense pubescence of spreading, straight trichomes. Subspecies *serpyllum* has appressed stems with a dense pubescence of irregularly twisted trichomes that are shorter than those found on subspecies *adhaerens.* A detailed treatment of this group is given in Herndon (1993).

*Chamaesyce garberi* complex

*Chamaesyce garberi* (Engelmann ex Chapman) Small, and *C. porteriana* Small have the erect, shrubby-branched growth habit of the *C. hyssopifolia* complex, but are distinguished by their cyathia solitary in leaf axils and thick leaves with entire margins.

*Chamaesyce garberi* as defined herein includes all populations of the complex with pubescent capsules. This includes *Chamae-*

*syce brachypoda* Small, *Chamaesyce mosieri* Small, *Chamaesyce keyensis* Small, and *Chamaesyce porteriana* var. *keyensis* (Small) Burch. There is variation within this complex that bears further study. In short, there appear to be three major groups with different pubescence patterns. These groups do not correspond to the species proposed by Small. Plants from the type locality at Cape Sable have long, spreading trichomes on the stem surfaces. The second densely pubescent group has strongly ascending to appressed, twisted trichomes. A final group is sparsely pubescent. In the extreme, the pubescence may be confined to the cyathia and capsules, suggesting a strong relationship with *C. porteriana.*

Small described *Chamaesyce keyensis* as a new species closely related to *C. porteriana* and Burch (1966) recognized the taxon as *C. porteriana* subspecies *keyensis.* An erect growth habit was primary reason for proposing these relationships. However, it escaped Small's notice that early collections of *C. garberi* from the type locality were sometimes erect. In fact, in both the *C. garberi* and *C. porteriana* groups, the basic growth habit of all plants seems to be erect. Often plants in both groups are found with a trailing growth, but these cases seem to be associated with litter that weights down the upper portions of the stems.

*Chamaesyce porteriana* Small is distinguished from *C. garberi* by its lack of pubescence. It superficially resembles large-leaved and sparingly branched, erect plants of *C. blodgettii.* See the discussion under the latter species for distinctions.

*C. scoparia* Small was recognized by Burch (1966) as *C. porteriana* var. *scoparia.* This name is applied to plants from the Lower Florida Keys that have narrow leaves and numerous, strictly ascending secondary branches. As currently defined, this presumptive variety grows sympatrically with plants that would be identified as *C. porteriana* var. *porteriana,* and cannot be upheld. There is a weak differentiation between mainland and keys populations of this species, and it is possible that all Keys populations should be recognized as var. *scoparia.* Small also recognized *C. adicioides* for highly branched plants with small leaves. I consider these to be no more than extemes of the natural variability in growth form of *C. porteriana.*

*Chamaesyce hirta* complex

*Chamaesyce hirta* (Linnaeus) Millspaugh and *C. ophthalmica* (Persoon) Burch are readily recognized by leaf shape and the

presence of two distinct trichome types on the stems. They also share very small, circular glands. The pedicels of the staminate flowers are exserted along the edges of the cyathium alternating with the glands and may be mistaken for gland appendages on superficial examination.

*Chamaesyce hirta* is the more robust plant with stems branching only at lower nodes, axillary inflorescences and small, but apparent, gland appendages.

*Chamaesyce ophthalmica* has smaller leaves than *C. hirta* in most cases, and dichotomous branches from the middle and upper nodes, and terminal inflorescences with no gland appendages. This species was called *C. gemella* (Lagasca) Small in most early floras.

*Chamaesyce hyssopifolia* complex

*Chamaesyce hypericifolia* (Linnaeus) Millspaugh, *C. hyssopifolia, C. lasiocarpa* and *C. nutans* (Lagasca) Small form a group with similar general appearance. Plants are annuals, usually erect, 30–70 cm tall, and shrubby-branched with spreading crowns. The leaves have conspicuously serrate margins and often have a cyanic spot near the center. In *C. hypericifolia* and *C. lasiocarpa,* the cyathia are clustered in essentially leafless axillary glomerules. In *C. hyssopifolia* and *C. nutans,* the cyathia are found in reduced, but recognizable, dichotomous branch systems. Glands are elliptic and small in all of these species. Gland appendages are usually larger than the glands and vary in color from white to pink (rarely red).

*Chamaesyce hypericifolia* was called *C. maculata* by Small (1933) and *Euphorbia glomifera* by Wheeler (1941). It is distinguished within the group by conspicuous, usually spreading, stipules that are much longer than wide.

*Chamaesyce nutans* may not occur in Florida. At the very least, Florida specimens referred to *C. hyssopifolia* and *C. nutans* are very closely related and probably not distinct. In particular, they both have a large, dark seed with 2–3 transverse ridges and one longitudinal ridge that give the seed a reticulate appearance. They also share a pattern of finely appressed puberulent stems and long, spreading trichomes on leaf surfaces. The capsule is glabrous in both regardless of pubescence on the stem. *Chamaesyce hyssopifolia* is often totally glabrous and at most has a small proportion

of stems pubescent near the tips. In *Chamaesyce nutans,* all stems are pubescent near the tips. This traditional distinction seems largely arbitrary, but is herein maintained pending a detailed study of the problem.

*Chamaesyce lasiocarpa* is densely puberulent in all parts. The pubescent capsule, in particular, distinguishes it within the complex. It is a recent introduction to Florida, apparently first collected in 1971.

*Chamaesyce maculata* complex

*Chamaesyce humistrata* (Englemann ex Gray) Small, *C. maculata* (Linnaeus) Small and *C. thymifolia* (Linnaeus) Millspaugh form a group apparently allied to the *C. dioeca* complex. They are characterized by long appressed trichomes on capsule, densely pubescent upper stem surfaces, glabrous lower stem surfaces, and separate stipules with long acuminate tips. All these species often have a large cyanic spot near the center of the leaf.

*Chamaesyce maculata,* called *Euphorbia supina* by Wheeler (1941), is distinctive within the group on account of the short styles that are conspicuously broadened near the tip. *Chamaesyce matthewsii* Small (Small 1933) is applied to plants of this species having internodes longer than the leaves. *Chamaesyce tracyi* is another name applied to some growth forms of these plants.

*Chamaesyce humistrata* is very similar to *C. maculata,* but more robust and with larger leaves, and longer, filliform styles. The formation of roots on the stems of *C. humistrata* is also distinctive.

*Chamaesyce thymifolia* is very similar to *C. maculata* in appearance, but has longer, filiform styles and more pointed leaves. In addition, the peduncle of the pistillate flower on this species is shorter than the involucre of the cyathium, so the capsule is not exserted. The involucre is ultimately flattened against the bottom of the capsule. The capsule is not fully exserted in all specimens of *C. maculata,* but the involucre is never crushed in these cases.

*Chamaesyce polygonifolia* complex

*Chamaesyce bombensis* (Jacquin) Dugand, *C. cordifolia* (Elliott) Small, *C. cumulicola* Small, and *C. polygonifolia* (Linnaeus) Small

form a group distinguished by their glabrous stems and lacerate stipules. *C. bombensis, C. cumulicola* and *C. polygonifolia* are further characterized by a rounded white seed.

*Chamaesyce bombensis* of this paper is often referred to *C. ammannioides* (H.B.K.) Small, but I believe the association between the former, earlier name and the species is correct. *C. bombensis* has also been treated as *C. ingallsii* Small. *C. bombensis* is the most common member of the complex in Florida and has a branching pattern usually resulting in plants with leaves and short stems concentrated near the distal quarter of the main stems. The cyathia are basically terminal, but often a single branch is produced below a cyathium so they appear to be axillary.

*Chamaesyce cordifolia* is distinguished within the complex in the more orbicular leaf shape, dense pubescence on the adaxial surface of the stipules and angled seeds.

*Chamaesyce cumulicola* has a diffuse branching pattern, and the cyathia appear to be axillary rather than terminal. In addition, the leaves are much narrower than those of the other species and have distinctive red margins. A fragmentary specimen from Escambia county was identified as this species by Burch, but the record needs confirmation before it can be accepted.

*Chamaesyce polygonifolia,* reaching its southern limits on the Northeast coast of Florida, has a distinctive appearance due to the obviously terminal position of the cyathia and the dichotomous appearance of the branching. In contrast to other species, glands are produced irregularly in the specimens of *C. polygonifolia* examined from Florida.

*Chamaesyce prostrata* complex

*Chamaesyce mendezii* (Boissier) Millspaugh and *Chamaesyce prostrata* (Aiton) Small share the peculiar pubescence pattern of spreading hairs concentrated on the angles of the capsule, densely pubescent upper stem surfaces, and glabrous lower stem surfaces. However, they differ greatly in seed surface sculpture, and may not be closely related. They are treated together here more as a matter of convenience than conviction.

*Chamaesyce prostrata* is characterized by small, dark green, orbicular leaves and red stems. Specimens are often mounted with the lower surface facing upward, so stem pubescence will appear

only along the sides of the stems. Called *Euphorbia chamaesyce* by Wheeler (1941).

*Chamaesyce mendezii* is lighter green and has larger leaves than *C. prostrata.* In addition, the stems of *C. mendezii* are evidently flattened, and there are two types of trichomes on the upper stem surface. Trichomes near the edges of the upper surface are long and spread out to the sides of the stems while trichomes in the middle of the upper surface are shorter and often appressed. This species is a recent introduction to Florida with the first known collection in 1954 (Burch 1965).

*Chamaesyce mesembryanthemifolia* (Jacquin) Dugand

A shrubby habit, fleshy leaves and conspicuous ligules are diagnostic for this species. Leaves are ascending and overlapping on the branches. This species is referred to *C. buxifolia* (Lamarck) Small by most earlier authors.

*Chamaesyce serpens*
(Kunth *in* Humbolt, Bonpland & Kunth) Small

Rooting stems, the small but conspicuous white ligule and the elongated, white perianth lobes are distinctive on this species. The leaf shape and habit of *C. serpens* are similar to *C. prostrata* and some specimens of *C. blodgettii,* but no other Florida species seem to be closely related.

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# THE CONTRIBUTIONS OF WILLIAM T. GILLIS (1933–79) TO THE FLORA OF THE BAHAMAS

LEE B. KASS AND W. HARDY ESHBAUGH

## ABSTRACT

William T. Gillis (1933–79) became interested in the Bahama flora while conducting field research for his Ph.D. His interest intensified from 1968 to 1972 during his appointment as taxonomist and herbarium curator at the Fairchild Tropical Garden in Miami, Florida, U.S.A. He made many collecting trips to the Bahama Islands, and in 1970, in collaboration with Richard A. Howard of Harvard University and George R. Proctor of the Institute of Jamaica, proposed to revise *The Bahama Flora* that Britton and Millspaugh had published in 1920. Although their NSF proposal was not funded, Gillis continued his work on the Bahama flora, as a Mercer Research Fellow at Harvard University, then as a Visiting Assistant Professor at Hope College, Holland, Michigan, and finally as Assistant Professor at Michigan State University, East Lansing. His publications for revisions of *The Bahama Flora* appeared between 1973 and 1977. Gillis' death in 1979, at the age of 45, prevented his completion of this valuable contribution to Bahamian natural history. A comprehensive summary of his contributions to the study of the Bahama flora is presented.

Key Words: William T. Gillis, The Bahama Flora, Natural History of the Bahamas

## INTRODUCTION

*The Bahama Flora,* the first complete flora of the Bahamas, was published in 1920 by Britton and Millspaugh. In their section "Exploration and Collections," they reported all known publications and botanical collections made from the early 1700's through 1911. In 1970, William T. Gillis, in collaboration with Richard A. Howard and George R. Proctor, proposed a revision of *The Bahama Flora,* and from 1973 until his death in 1979, Gillis published many contributions toward this goal.

In 1982, Correll and Correll published *Flora of the Bahama Archipelago,* a taxonomic work that systematically describes and illustrates the plants of the Bahamas. Although the Corrells credited various collectors and field workers, in their preface, they did not present an exhaustive list of publications and collections as did Britton and Millspaugh in *The Bahama Flora.* Also, the Correll's *Flora* lacked a comprehensive bibliography, an omission that came to our attention while we were preparing vegetation field guides for Andros (Nickrent et al., 1983) and San Salvador

(Kass, 1991) islands, Bahamas. The Correll's bibliography is "selective." Specifically, many of the publications of Gillis and collaborators, as well as those of other investigators (e.g., Lewis, 1971), were not cited.

William T. Gillis' contribution to the flora of the Bahamas has been neglected and not fully appreciated. This paper provides a comprehensive summary and interpretation of his studies of that flora.

## PERSONAL LIFE AND EDUCATION

William Thomas Gillis, Jr. (1933–79, Figure 1) was born on 22 June 1933, at Perth Amboy, New Jersey. He received his B.A., with honors, from Rutgers University in 1955. His master's thesis project was an ecological study of seed germination patterns of sand dune plants in Michigan and New Jersey, for which he received an M.S. in plant ecology from Michigan State University in 1957. It was another 13 years before he was able to complete his Ph.D. work, because of his heavy teaching load, many extracurricular interests, and a commitment to family duties (pers. comm., J. H. Beaman, 20 July 1993; R. K. Rabeler, 19 July 1993; Denise Birmingham, 10 June 1993).

His doctoral research, supported in part by a grant from the National Institutes of Health, was an exhaustive study of the systematics and ecology of the poison-ivies and the poison-oaks, species of the genus *Toxicodendron* (Anacardiaceae). Gillis became interested in the flora of the Bahamas when he conducted field research in the Bahama Islands, beginning in 1963, for this dissertation research (Anon., 1968; letter from R. A. Howard to L. Kass, 23 March 1993; Table 1). "He returned several times to the Bahamas for the specific purpose of studying the flora and collecting specimens for the Michigan State University Herbarium. He spent several weeks collecting on Rum Cay, one of the more remote islands in the Bahamas which had been little studied botanically previously" (Anon., 1968; Table 1). He had an extensive publication list before he completed his dissertation work (Gillis, 1970b). His Ph.D. was granted in 1970 by Michigan State University. In 1972, Gillis received the Jesse M. Greenman Award in recognition of the best published paper in plant systematics based on a doctoral dissertation (Gillis, 1971a–d; Stafleu, 1972).

Figure 1. William T. Gillis. Michigan State University Photographic Laboratory, Information Services. Negative #682043-1. Courtesy of J. H. Beaman.

A detailed biography of W. T. Gillis is currently in preparation (L. B. Kass, R. K. Rabeler, and W. H. Eshbaugh).

## CONTINUED INTEREST IN THE BAHAMA FLORA

Gillis' interest in the flora of the Bahamas was solidified when, in 1968, he took a six-week Summer Seminar in Tropical Botany,

Table 1. Itineraries for W. T. Gillis' collections in the Bahamas, and the Turks and Caicos Islands, 1963–1978. All data were compiled on 21 July 1993 by L. B. Kass and R. E. Hunt from the field notebooks of W. T. Gillis, deposited at MSC.

| | |
|---|---|
| | 1963 |
| 19–21 March | New Providence (5253); Eleuthera, Rock Sound (5254–5255); San Salvador (5256–5336). |
| 22–24 March | New Providence (5337–5357). |
| | 1966 |
| 15–18 March | New Providence (6074–6088); Andros (6089–6133); Abaco (6134–6183). |
| 19–25 March | San Sal (6184–6224, 6301–6312); Rum Cay (6225–6300). |
| | 1967 |
| 5–6 March | New Providence (6355–6370); Andros (6371–6414). |
| | 1968 |
| 28–31 December | New Providence, Paradise Island (7299–7306); Abaco (7307–7422). |
| | 1969 |
| 1–2 January | Abaco (7423–7452); New Providence (7453–7499). |
| 31 March–1 April | Grand Bahama (7735–7868). |
| 7–9 July | New Providence (8331–8395). |
| 23 October | Grand Bahama, Freeport (8568–8509). |
| 29–31 December | New Providence (8706–8712); San Salvador (8713–8763). |
| | 1970 |
| 1–4 January | San Salvador (8798–8855); New Providence (8856–8864). |
| 4 May | New Providence (9183–9207). |
| 9–12 June | Exuma (9332–9382); Great Exuma (9383–9414). |
| 19–26 April | New Providence (10595–10706); Acklins (10707–10730); Crooked Island (10731–10738). |
| | 1972 |
| 28 February–4 March | Bimini (11275–11314). |
| 3–4 July | Andros (11385–11403). |
| | 1973 |
| 7–20 February | Mayaguana (11527–11623); Inagua (11648–11778). |
| 21–26 February | Turks and Caicos: Grand Turk (11779–11796, 11850–11859); Pine Cay (11797–11832); North Caicos (11833–11849); Salt Cay (11860–11880). |
| 13–15 November | New Providence (11889–11914). |

Table 1. Continued.

| | |
|---|---|
| | 1974 |
| 21–23 May | Great Ragged Island (11915–11928); Little Ragged Island (11929–11962); Exuma (11963–11974). |
| 24–27 May | New Providence (11975–11995); South Andros (11996–12036, 12044–12050). |
| 27 May–7 June | Inagua (12037–12043, 12051–12180). |
| 9–19 June | Turks and Caicos: North Caicos (12181–12230); Middle Caicos (12248A–12272, 12282–12315); Grand Turk (12273–12281, 12316–12357). |
| | 1975 |
| 1–6 April | Turks and Caicos: Providencials (12365–12378); West Caicos (12379–12472). |
| 9–10 July | South Andros (12505–12534); Vicinity of Congo Town (12535–12565); Vicinity of Kemps Bay (12565A–12598). |
| | 1976 |
| 1–3 January | New Providence (12788–12791); South Andros (12792–12820); Cay Sal (12821–12855). |
| 27 February–6 March | Andros (12856–12906); South Andros (12907–12922); Green Cay (12923–12956); Exuma Chain (12957–12958); Little Farmers Cay (12959–12973); Exhuma (12974–13007). |
| 6–9 March | Rum Cay (13008–13094). |
| 9–14 March | Inagua (13095–13099); Little Inagua (13102–13153). |
| 17–18 March | Acklins (13153–13173); Crooked Island (13174–13208). |
| 21–24 March | Long Island (13209–13242); New Providence (13243). |
| | 1977 |
| 11–14 June | Eleuthera (13753–13843). |
| | 1978 |
| 28 March–4 April | New Providence (14390–14407); Turks and Caicos: East Caicos (14408–14495); South Caicos (14496–14498, 14514–14526); Grand Turk (14499–14513). |

offered for the first time by Richard A. Howard of the Arnold Arboretum, Harvard University, Howard Teas of the University of Miami, and, P. Barry Tomlinson of the Fairchild Tropical Garden (FTG). This seminar was held at the Garden in Miami (Coral Gables), Florida, and jointly sponsored by the University of Miami and the FTG (Popenoe, 1968; Anon., 1968; Figure 2).

Figure 2. GROUP PICTURE OF SEMINAR IN TROPICAL BOTANY. Standing, left to right: Thomas Armentano, Dr. R. A. Howard, Robert Stewart, L. Ramos-Lendon, A. Gentry, S. Donachie, Kiat Tan, Dr. J. Popenoe, Dr. H. Teas, Dr. P. B. Tomlinson, R. Vagner. Squatting, left to right: W. T. Gillis, L. Pardue, Mrs. D. Smullen, Dr. I. J. McClurkin Jr., Miss E. Jackson, W. Kirk. Reprinted, with permission, from Fairchild Tropical Garden Bulletin 1968. 23: 5.

His research paper for that course was a study of some of the unusual genera represented in the living "Bahama Collection" at the Garden (letter from R. A. Howard to L. Kass, 3 Nov. 1992). This research project, a very supportive recommendation from Howard to John Popenoe, director of the Garden, as well as Gillis' exhaustive plant systematic doctoral dissertation, qualified him for the position of taxonomist at FTG, which he began on 1 October 1968 (letter from Gillis to H. E. Moore, Jr., 10 Oct. 1968; Anon., 1968; Stafleu, 1969; letter from R. A. Howard to L. Kass, 3 Nov. 1992).

In 1969, the FTG herbarium "became active" (Gillis, 1969) with the appointment of William T. Gillis as curator, allowing for its expansion in a new direction—that of plants of the Bahama Islands (Gillis, 1969; Stafleu, 1969). In the newsletter of the Botanical Society of America, Gillis (1972) published a comprehensive summary of the importance of the FTG, its staff, gardens, and herbarium and described the significance of the Garden's Bahamian collection. While on the staff at FTG, Gillis was made

Adjunct Assistant Professor in the Department of Biology at the University of Miami, Coral Gables, Florida. This appointment continued through 1974.

While he was the taxonomist and curator at FTG, Gillis lived in a cottage at the Kampong (Sweeney, 1969), former home of David Fairchild, for whom the FTG was named. Fairchild's home had been purchased in 1963 by Edward Cleaveland and Catherine Hauberg Sweeney, who gave the property, in 1984, to the Pacific Tropical Botanical Garden (Schokman, 1985; name changed to National Tropical Botanical Garden in 1988). Catherine Sweeney, a member of the FTG Board of Trustees and a patron of the Garden, supported Gillis financially in many of his scientific endeavors (Anon., 1970). Gillis contributed to the newsletter *Kampong Notes* between 1969 and 1979.

Under the auspices of the FTG, between 1969 and 1972, Gillis made collecting trips to the Bahama Islands (Table 1). In March/April 1969, he visited Grand Bahama to help a researcher "determine which plants are being made primary food source of several bird species" (letter from Gillis to H. E. Moore, Jr., 20 March 1969). On returning from this trip he wrote to H. E. Moore, Jr., director of the L. H. Bailey Hortorium (BH) at Cornell University (7 April 1969), that his Bahama trip was most worthwhile. He wrote that he had collected about "130 numbers, stripping the countryside as is my wont" and added that he had no place to put the specimens until new cases arrived.

In December 1969, he visited San Salvador "to collect herbarium specimens to record the plants living on the island, part of a larger project in rewriting the flora of the Bahama Islands" (Gillis, 1970a). He reported that this trip had a "thread of urgency," as "75% of the island" had been purchased for development and he feared that "many good collecting sites" would soon disappear. He hypothesized that there had been little change in the vegetation on the island since the early part of the century, when David Fairchild and P. H. Dorsett had visited that part of the Bahamas. He described the island and compared it with what Christopher Columbus may have observed in 1492. He reported that "many of the plants which Columbus described are still found on San Salvador," and specimens of these are in the FTG herbarium. On that same trip, at French Bay on the southern part of San Salvador, Gillis (1970a) reported that he had collected a specimen of *Coccothrinax* [*argentata* (letter from Gillis to H. E.

Moore, Jr., 27 Jan. 1970)] that was not silvery on the lower leaf surface. Gillis sent the plant to Robert W. Read, who identified it as *C. inaguensis* R. W. Read (Gillis, 1970a; Read, 1966). This was the first record of the plant from San Salvador, and seeds of the palm were brought back to FTG to grow. Specimen labels of *Wedelia behamensis* (seen at BH/CU in 1991, on loan from FTG, collection numbers 8759 and 8778) also collected by Gillis on San Salvador in 1969 suggest that he had a total collection of over 8000 plants by that time.

While Gillis was engaged in the Summer Seminar in Miami, just prior to his employment at FTG, Howard suggested that he "apply for the post [of taxonomist] at FTG and together [they] would prepare a Bahama Flora" (Gillis, no date; Gillis, 1969; R. A. Howard, pers. comm., 4 Aug. 1993). After his appointment as taxonomist Gillis wrote to Howard that George R. Proctor of the Science Museum of Jamaica, had been approached by the Bahamian government "about writing a new flora" with the possibility of the government underwriting part of it and that "he was willing to collaborate" (letter from Gillis to R. H. Howard, 31 July 1969). In December 1970, Gillis, Proctor, and Howard submitted a proposal to the National Science Foundation (NSF), proposing to prepare "a Manual and a Flora of the Bahama Vascular Plants" (Anon., 1970; Gillis, 1970b). Gillis, as principal investigator, requested support for five years and noted that "A promise of $17,000 toward publication was made by the Ministry of Agriculture and Fisheries, government of the Bahama Islands" (Anon., 1970; letter from O. S. Russel, Permanent Secretary to Gillis, 21 Oct. 1970; Gillis, 1970b).

On 6 August 1971, Gillis wrote to his collaborators, Howard and Proctor, that he had received a letter from NSF (letter from H. J. Carlson to Gillis, no date) that the grant proposal had not been funded. This rejection did not weaken his determination to continue his study of the Bahama flora. In that same letter to his colleagues, he solicited advice from Howard and Proctor on how to proceed: "Is it desirable to re-write the proposal . . . ? . . . Should we try another granting agency?" Howard responded with suggestions for revisions to the NSF. He also suggested applying to Sigma Xi or the American Philosophical Society, the Stanley Smith Trust, and "Archbold" (letter from R. A. Howard to Gillis, 9 Aug. 1971).

It is possible that the rejection of this grant proposal was a catalyst in the development of Gillis' unpleasant relationship with the management of the Fairchild Garden, but probably the main factor leading to his abrupt dismissal on 21 April 1972 (memo from J. Popenoe to Gillis, 21 April 1972) was simply a result of personality dissonance ("differed . . . on professionalism" and "incompatibility," United States Civil Service Commission, Form 171, W. T. Gillis, 7 July 1973) between Gillis and J. Popenoe, the director of the Garden. At any rate, Gillis vowed he would continue with and complete his "Flora." Popenoe, however, insisted that the project belonged to the Fairchild Tropical Garden, and he proceeded to recruit Donovan S. Correll to write the "Bahama Flora." Thus two rival projects, covering the same territory, proceeded simultaneously, leading eventually to considerable hostility between the principal investigators (G. R. Proctor, pers. comm., 4 June 1993).

While Correll was Program Director for Systematic Biology at the NSF (July 1971–July 1973), Harve J. Carlson, Divisional Director, Biological and Medical Sciences, endorsed a request from Correll "for permission to submit a research proposal in August 1973" to the NSF, immediately following his "tour of duty with the National Science Foundation at the end of July 1973" (letter from H. J. Carlson to the Director via the Deputy Assistant Director for Research, 11 Aug. 1972). Permission was granted by H. Guyford Stever, Director, NSF, for Correll to submit a proposal immediately upon the termination of his appointment (Correll, 1973). Correll was appointed taxonomist at FTG on 1 September 1973 (Anon., 1973; Correll, 1973). Correll's proposal (No. P4B0945) titled "Illustrated Vascular Flora of the Bahama Islands," submitted to NSF (Correll, 1973), dated 1 October 1973, was granted by NSF's Program in Systematic Biology, to begin on 15 November 1973, for "support of the project entitled 'Vascular Flora of the Bahama Islands,' . . . under direction of Donovan S. Correll" (Correll, 1973; letter from G. L. Ellis, Grants officer, to H. E. Kendall, President, FTG, no date, stamped 6 Dec. 1973; NSF Project Summary, NSF Grant No. GB-41190X, no date, stamped 6 Dec. 1973; Correll and Correll, 1982; letters from R. A. Howard to L. Kass, 3 Nov. 1992, and 23 March 1993). Donovan S. Correll and Helen B. Correll began their field collecting in the Bahamas in November 1973, and terminated col-

lecting in November 1980 (Correll and Correll, 1982). The culmination of their work was the publication of the *Flora of the Bahama Archipelago* in 1982.

In 1973, Gillis wrote to Correll offering to "assist [him] in any way that [he could] as [he] assum[ed his] post at Fairchild" (letter from Gillis to D. S. Correll, 7 March 1973). In that same letter Gillis indicated to Correll that Howard, Proctor, and he were working on a "field guide and flora of the Bahama Islands." Even after leaving FTG, Gillis continued to deposit specimens in its herbarium, specimens he had collected while taxonomist there (letters from Gillis to D. S. Correll, 9 Jan., 28 Feb., 14 July, 7 Aug. 1974; 12 July, 4 Nov. 1975; 6 April 1977).

## RESEARCH FELLOW AT THE ARNOLD ARBORETUM, HARVARD UNIVERSITY, AND THE BAHAMA FLORA

In 1972, Gillis went to the Arnold Arboretum at Harvard on a Mercer Research Fellowship to work full time on the Bahama flora (letter from H. E. Moore, Jr. to Gillis, 12 June 1972; letter from Gillis to H. E. Moore, Jr., 11 April 1973). During this two-year period (1972–74), while a fellow at the Arnold Arboretum, Gillis made many visits to the Bahamas (Table 1). His collections and investigations during this short time led to 13 scientific publications over five years (Gillis, 1974a, 1974b, 1974c, 1976a, 1976b; Gillis and Proctor, 1974, 1975a, 1975b; Gillis and Stearn, 1974; Gillis et al., 1973, 1975a, 1975b; Mears and Gillis, 1977). His research and field trips while he was at Harvard were supported by a grant to the Arnold Arboretum from an anonymous donor interested in the Bahama flora and by a grant from the National Geographic Society (Beaman, 1982). After leaving Harvard in 1974, he continued to collect data and publish on the Bahama flora until his death in 1979.

In a 1973 publication, Gillis, Howard, and Proctor recognized 81 taxa of vascular plants as additions to the "Bahama flora since the publication of Britton and Millspaugh's work (1920)." In that publication they presented a compilation of additional vascular plants, growing without cultivation, in the Bahama Islands, including the Turks and Caicos group, while they were "in the process of preparing a new vascular flora of the Bahama Islands" (Gillis et al., 1973). Many of these additions to the flora were reported for the first time and were based on personal collections,

new collections made available to them, and reports from the literature (Gillis et al., 1973). The principal works they cited were Howard (1950), Howard and Dunbar (1964), and Lewis (1971). Herbarium specimens for plants reported for the first time in their paper were, unless otherwise designated, deposited at FTG (Gillis and John Popenoe specimens), the New York Botanical Garden (NY, Howard specimens), and the Institute of Jamaica (IJ, Proctor material), with duplicates at the Arnold Arboretum (A). Of the 81 additions to the flora, 24 specimens comprising 19 new records were vouchered by Gillis, two of these from San Salvador. Nineteen of Gillis' 24 voucher specimens were recently located at the FTG herbarium (L. Kass, 7–10 June 1993).

One year later, Gillis (1974a) again reported that he was "working in collaboration with Richard A. Howard of the Arnold Arboretum and George R. Proctor of the Institute of Jamaica towards a revision of Britton and Millspaugh's 'Bahama Flora,' published first in 1920 and reprinted without changes in 1962." In this same publication Gillis "offers updated annotations on the correct scientific names to be applied to the species listed by Britton and Millspaugh whose work was completed under the provisions of the American Code of Botanical Nomenclature." He encouraged other researchers to use his list and to report changes or additions to him. He referred the reader to other lists of nomenclatural corrections for island floras in the Caribbean and emphasized that the reasons for the changes of names are not always explained, so that investigators must reinvestigate each and every problem. In this study, however, Gillis (1974a) provided explanations for all name changes he had made. When name changes were made by others, he cited the publication on which that information was based. The study reported name changes for species in 85 vascular plant families. For ease of reference he followed the order of Britton and Millspaugh's *Bahama Flora,* with citations to the page numbers on which species were found. Revised keys to a few of the species were also included.

With the intent of continuing to revise *The Bahama Flora,* in collaboration with Proctor and Howard, Gillis (1974b) examined much of the material available to Britton and Millspaugh, especially type specimens, by visiting herbaria in both the United States and in Europe. Using this research, Gillis (1974b) presented "a union of species resulting from a broader approach to species concepts than employed" by Britton and Millspaugh (Gillis and

Proctor, 1975a). Gillis believed that many of Britton and Millspaugh's "species" were phantoms. These phantoms, he explained, were not really species at all because they were based on minor variations among specimens. Because Britton and Millspaugh's *Bahama Flora* recorded so many new "species," 12 percent of their flora was reported to be endemic. Gillis (1974b) argued that the geologic time span since the island flora were established was too short for this amount of endemism to have developed. Because the Bahamas were surrounded on three sides by nearby land masses, which had contributed most of the fauna and flora, it appeared to him that those species labeled "endemic" in *The Bahama Flora* of Britton and Millspaugh would be found in other neighboring floras, under earlier names, if one were to look for them. He presented evidence on why 28 species names in *The Bahama Flora* considered to be endemic should be reduced to species that are also present in Cuba, Hispaniola, and Florida. Correll and Correll's *Flora* (1982) did not include many of the changes Gillis (1974b) suggested, and thus kept the number of apparent endemics in the Bahamas high. Gillis' lower number of endemics is probably more realistic.

## APPOINTMENT AS ASSISTANT PROFESSOR AT HOPE COLLEGE AND CONTINUED PUBLICATIONS ON THE BAHAMA FLORA

In 1974, Gillis was appointed Visiting Assistant Professor at Hope College in Holland, Michigan (letter from Gillis to H. E. Moore, Jr., 20 Aug. 1974) and continued to work on revisions of *The Bahama Flora.* He also taught summer classes at the Kellogg Biological Station and "May term" classes in Tropical Botany at the Kampong and environs (letter from Gillis to D. S. Correll, 14 April 1975). For his course at the Kampong, he drafted "a textbook of tropical botany" that he hoped to publish with "Drs. Richard A. Howard and P. Barry Tomlinson of Harvard University, [his] mentors in tropical botany" (Gillis, unpublished 'Disclaimer' from "a textbook of tropical botany," May 1976).

Continuing with studies of the Bahama flora, Gillis and Stearn (1974) recommended a name change for *Mimosa latisiliqua* L. based on their investigation of Linnaean materials. They interpreted the International Code of Botanical Nomenclature as requiring a Linnaean binomial to be essentially the selection of "the

specimen or illustration from which Linnaeus obtained the information embodied in his diagnostic phrase-name" (Blunt and Stearn, 1971, as cited by Gillis and Stearn, 1974). Their evidence led them to conclude that the correct name should be *Leucaena latisiliqua* (L.) Gillis, *comb. nov.*, which they considered a synonym of *Leucaena leucocephala* (Lam.) de Wit. De Wit (1975) rejected their argument and presented evidence for retaining his previously corrected name (De Wit, 1961). Correll and Correll (1982) adopted de Wit's combination. Disagreement remains as to which name should apply.

While collecting in the southern Bahama Islands in 1973, Gillis and Proctor (1974) located a specimen of *Caesalpinia* (*Guilandina* of Britton and Millspaugh) that they believed was "distinct from others indigenous to the Bahamas." They described this as a new species and named it *Caesalpinia murifructa* Gillis & Proctor. It was included by the Corrells in their *Flora* (1982), who noted that it probably should be considered a variant of *C. ovalifolia.*

While Gillis was collecting plants and revising plant names for preparation of a new vascular flora of the Bahama Islands, he was also attempting to understand the distribution patterns of organisms related to the geological and natural history of the Islands (Gillis et al., 1975a; Gillis, 1977c), and had compiled a bibliography for such a purpose. During the same time, Roger Byrne and Wyman Harrison had independently compiled a bibliography for the Bahamas. They therefore proposed to cooperate, pool their resources, and publish their results together. The result was the publication of the *Bibliography of the Natural History of the Bahama Islands* in 1975. This work includes six of Gillis' publications through 1974, and is one of two Gillis publications cited in the "Selected References" of Correll and Correll (1982). From the introduction to this *Bibliography* we learned that Gillis had recently contributed a monthly column on native plants to *Conch News,* a weekly newspaper of the Turks and Caicos Islands.

Another finding from Gillis' field studies in the southeastern Bahamas in 1973 through 1976 was the discovery of an indigenous population of *Roystonea* on Little Inagua (Gillis et al., 1975b; Gillis, 1977a, 1977b, 1977e). Gillis et al. (1975b) reported that this palm was known to Britton and Millspaugh in the Bahamas "only as a planted tree." Gillis, Proctor, Avery, and Proctor's field assistant Errol Scott observed these palms while flying over the islands on their way to Grand Turk (G. R. Proctor, per. comm.,

4 June 1993). The palms were restricted to sinkholes and were growing with *Sabal.* From fruit specimens collected by Donald Buden in 1975, Robert Read determined the palms to be *Roystonea.* In 1976, Gillis, serving as botanist, along with Harry Clench (entomologist), and Arthur Bianculli (herpetologist), hiked back from the coast of Little Inagua Island to visit these royal palms. They were members of an expedition led by Mary Clench (ornithologist) from the Carnegie Museum of Natural History "to locate the endangered Kirtland's warbler" in the Bahamas (Anon., 1976; Gillis, 1977a, 1977b, 1977e). Gillis reported that the palms appeared to be royals of Hispaniolan affinity, *Roystonea hispaniolana* Bailey. This identification was confirmed by Read (letter from R. W. Read to Gillis, 17 Jan. 1977). This 1976 expedition was sponsored by the World Wildlife Fund and the M. Graham Netting Fund of the Carnegie Museum.

Gillis and Proctor (1975a) published a second compilation of additions and corrections to Britton and Millspaugh's *Bahama Flora,* acknowledging 1974 reports of new species by botanical investigators D. S. Correll, and S. R. Hill. They deposited herbarium voucher specimens at A, the Gray Herbarium (GA), and IJ. They reported 20 plants new to the Bahama flora, 9 of which were vouchered by Gillis, and they explained the change of name for an additional 22 species, again reducing the number of alleged endemics in the Bahamas. Five of the 22 name changes were corrections to names in Gillis' (1974a) previous publication for name changes in the Bahama flora.

During the years 1974–77, in his quest for accurate application of scientific names in revising *The Bahama Flora* of Britton and Millspaugh, Gillis investigated many Bahama species. Gillis (1974c) investigated *Spermacoce confusa* Rendle because he believed that the name had not been validly published. Howard (1989), however, later reported that investigations by Nicolson (1977, J. Arnold Arb. 58: 445–447) revealed that previously published Latin descriptions had been published for this species name. Ward and Gillis (1975) examined *Sisyrinchium* and thanked D. S. Correll, among others, for assistance in locating and lending specimens for study. Their revision was incorporated in *Flora of the Bahama Archipelago* (Correll and Correll, 1982). Gillis additionally investigated *Polygala* (Gillis, 1975), *Agave* (Gillis, 1976a), and *Pluchea* (Gillis, 1977f), but these treatments were not cited by the Corrells (1982). The mistletoes *Dendropemon*

and *Phoradendron* (Gillis, 1976b), were investigated, but the Corrells (1982) did not accept Gillis' treatment contributing to their recognizing a high number of endemics for the Bahama flora. Genera in the subfamily Gomphrenoideae of the family Amaranthaceae (Mears and Gillis, 1977), were also studied; and Correll and Correll (1982) incorporated some of these name changes.

During this same period, Gillis and Proctor (1975b) made a collection of wood samples from 37 specimens of Bahama trees and shrubs taken from 5 islands in the Bahamas. They deposited these specimens in the Wood Laboratory at Harvard University, along with herbarium voucher specimens at A and IJ. Many of these specimens had not been placed on permanent file or photographed before. The nomenclature for the species followed Britton and Millspaugh (1920), as modified by Gillis (1974a, 1974b).

Gillis' (1976d) third publication, in collaboration (but not coauthorship) with Proctor, on additions and name changes to the Bahama flora, involved 34 name changes and added 9 species not previously reported from the islands. The Corrells (1982) incorporated many of these changes reported by Gillis in this work. For one of the names they did not change, *Cephalocereus Millspaughii,* they noted "the species are separated on tenuous, recondite characters and probably should be combined (Correll and Correll, 1982, p. 1004); for these reasons Gillis had already combined them and changed the name in 1976. One of the additions reported by Gillis in 1976d was collected on San Salvador Island by Robert R. Smith. The new plant, *Aechmea lingulata* L. Baker, represented both a new species and a new genus to the Bahama flora. The voucher specimen was deposited in the Hoystradt Herbarium of Hartwick College (HHH). Gillis' study was supported from travel funds granted by Hope College and the Society of Sigma Xi.

Afforded the opportunity to visit Cay Sal in 1976, Gillis (1976c) specifically investigated the Compositae because he had seen and mapped distributions of all species (Percy) Wilson had collected in 1907 for Britton and Millspaugh's *Bahama Flora* project, and Gillis knew that few members of this family had been collected on Cay Sal prior to 1976. Gillis observed four ubiquitous species of composites found on Cay Sal and the western Bahamas. He also reported finding Red Mangrove, not previously recorded there. He noted the uncommon prevalence of *Cynanchum bahamense,* a milkweed vine (Asclepiadaceae), as fitting a pattern

known for insular biotas, exploiting the available niche, and being "phenomenally abundant" (Gillis, 1976c).

What intrigued him more, however, were the plants that he would *not* find on the island. He listed 18 species of common plants found throughout the Bahamas that he expected to find but were absent from Cay Sal. He attributed the island's depauperate flora to its size and distance from any other island source, making it "a small target for any successful invasion of seeds from Cuba, Florida, the rest of the Bahamas, or . . . even more distant lands" (Gillis, 1976c). He deposited plants collected on Cay Sal at IJ, A, and the Botanical Garden in Nassau.

In 1977d, Gillis contributed a chapter titled "Biogeography and Vegetation" to the Land Resources Study in the Bahamas, an investigation into the land and water resources of the Bahama Islands. The study was carried out by the Bahamas Land and Resource Survey between 1969 and 1975. The section Gillis contributed provided a setting for the survey's vegetation studies. A summary of the biogeography is presented at the end of the chapter; one of his conclusions is an important warning that the effect of human interference had been to reduce the height of the woodland and decrease the number of species. He cautioned potential developers, who might undertake haphazard clearing, of the slow regeneration of vegetation cleared for farming. He included four photographs of the vegetation on Abaco, Inagua, Eleuthera and North Andros.

While visiting herbaria for his own studies, Gillis generously offered his time to other investigators. For example, a study proposing the conservation of the generic name *Picrodendron* Grisebach, endemic to the West Indies, was supported by the efforts of Gillis "who did much of the herbarium work in Europe" (Hayden and Reveal, 1980) and who supplied specimens for an anatomical study by W. J. Hayden (1977). Although the proposed conserved name was not adopted by Correll and Correll (1982), the proposal to conserve (No. 4134) was accepted in 1984 (Nicolson, 1984).

## APPOINTMENT AS ASSISTANT PROFESSOR AT MICHIGAN STATE UNIVERSITY, AND ASSOCIATION WITH THE KELLOGG BIOLOGICAL STATION

On 1 September 1977, Gillis was appointed Assistant Professor in the Natural Science Department at Michigan State University,

East Lansing, with joint appointments in the Department of Botany and Plant Pathology and the Kellogg Biological Station (letter from J. H. Beaman to W. H. Eshbaugh, 11 May 1993; Cowan, 1979). He was also awarded staff privileges at the Field Museum of Natural History, Chicago. Although he had been advised of a health problem and warned of the need for urgent corrective surgery in January 1979, he chose to teach two scheduled summer courses before surgery, rather than disappoint his students (R. K. Rabeler, pers. comm., 21 June, 19 July 1993). Unfortunately, this dedication to his students led to a fatal heart attack on 20 June 1979, while he was teaching at the Kellogg Biological Station (Cowan, 1979).

At the time of his death, Gillis was engaged in a number of research projects concerning the Bahama flora. One of these projects, in collaboration with Proctor, was a revision of the genus *Caesalpinia.* The investigation was not published, but Proctor (1982) reported their unpublished conclusions for Jamaican species.

A second project, in collaboration with Howard, involved an investigation of 15 names from the *Prodromus Plantarum Indiae Occidentalis* (1825) of William Hamilton (1783–1856), names not included in *Index Kewensis* or its supplements (letter from Gillis to R. A. Howard, 27 June 1976; Howard et al., 1981). This work was relevant to revisions of both the *Bahama Flora* and the *Flora of the Lesser Antilles,* since "names not having been indexed in I. K." had been used again (letter from Gillis to R. A. Howard, 27 June 1976).

Gillis and Correll never met "face to face" (letter from Gillis to D. S. Correll, 15 June 1977). Although some members of the FTG staff were led to believe that Correll tried to contact Gillis about collaborating on investigations of Bahama flora without success and that he tried to locate Gillis' specimens and notes after his death, again unsuccessfully (records of phone conversations and letters to L. B. Kass archived at ECH), correspondence between the two men suggest this is not the case. Between the years 1973 and 1977, Gillis attempted to resolve the apparent conflict between them (letters from Gillis to D. S. Correll, 7 March 1973; 14 April, 12 July, 25 August, 4 Nov. 1975; 15 May 1976; 15 June 1977). Correll's existing correspondence to Gillis, however, did not indicate that he responded to these overtures (letters from D. S. Correll to Gillis, 19 April, 16 July 1975; 20 June 1977).

Gillis' unpublished research materials are archived at the Michigan State University Beal-Darlington Herbarium (MSC; letters from J. H. Beaman to W. H. Eshbaugh, 7 May, and 11 May 1993). The distribution maps Gillis referred to in his paper on Cay Sal (1976c) were accessible to Eshbaugh, who published Gillis' distributions for *Capsicum annuum* L. var. *aviculare* (Dierb.) D'Arcy & Eshbaugh and *Scaevola plumieri* (L.) Vahl in the Bahamas (Eshbaugh, 1987; Eshbaugh and Wilson, 1986). In July 1993, Kass examined the entire three volumes of distribution maps that Gillis (unpubl.) prepared for the Bahamas. Kass also located Gillis' correspondence, research materials, and field notebooks for his work on the flora of the Bahamas (L. B. Kass visit to MSC, 20–21 July 1993).

## SUMMARY AND CONCLUSIONS

William T. Gillis, together with George R. Proctor and Richard A. Howard, intended to publish a revision of *The Bahama Flora* of Britton and Millspaugh. To this end Gillis spent much time investigating the flora in the field, visiting herbaria around the world, and searching the literature. Gillis' publications make clear that he was a fair and fastidious researcher who carefully explained and documented his conclusions and always credited those who did the work. Howard, former director of the Arnold Arboretum, wrote that Gillis' "taxonomic judgement was quite good [and that] he could use a library to perfection" (letter from R. A. Howard to L. Kass, 3 Nov. 1992). Unfortunately, because of his untimely death at the age of 45 his goal was not achieved. Sadly, the brief notice of his death to the scientific community did not mention his work in the Bahamas (Cowan, 1979). Scholars who wish to examine Gillis' research materials will find them available at MSC.

Correll and Correll (1982, p. 1609) state in the preface to their "Selected References" that they included only "revisions, monographs, and pertinent Floras that have been useful to [them], and can be useful to others. Numerous papers, including [their] own, have been published that give new additions to the flora, nomenclatural changes, and other minor details. These are not included." This was an unfortunate decision, for it deprives users of their *Flora* ready reference to, and a complete appreciation of,

the work published prior to 1982. In particular, many of Gillis' papers are not included.

The authors of this paper (on the basis of twenty years work with the flora of the Bahamas) have found that the work of Gillis and his collaborators has added significantly to our understanding of the flora of the Bahamas. We anticipate that their contributions will now be recognized and appreciated by future scholars of the Bahama flora.

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## DEDICATION

This paper is dedicated to Dr. Catherine H. Sweeney, for her interest in the Bahama flora.

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# NEW TAXA AND NEW NOMENCLATURAL COMBINATIONS IN THE UTAH FLORA

STANLEY L. WELSH


## ABSTRACT

This paper includes the results of investigations leading to a revision of *A Utah Flora* by Welsh, Atwood, Goodrich, and Higgins, a publication whose first edition published in 1987 is now out of print. The following new taxa and nomenclatural combinations are proposed, based on plants from Utah and from northern Arizona: *Mertensia lanceolata* (Pursh) DC. var. *coriacea* (A. Nels.) Higgins & Welsh, *comb. nov.*; *Arenaria rubella* (Wahl) J. E. Sm. var. *filiorum* (Maguire) Welsh, *comb. nov.*; *Zuckia brandegei* (Gray) Welsh & Stutz var. *plummeri* (Stutz & Sanderson) Welsh, *comb. nov.*; *Ambrosia sandersonii* Welsh, *sp. nov.*; *Agoseris glauca* (Pursh) Raf. var. *cronquistii* Welsh, *var. nov.*; *Artemisia campestris* L. var. *petiolata* Welsh, *var. nov.*; *Haplopappus lignumviridis* Welsh, *sp. nov.*; *Hymenoxys acaulis* (Pursh) Parker var. *nana* Welsh, *var. nov.*; *Senecio castoreus* Welsh, *sp. nov.*; *Senecio musiniensis* Welsh, *sp. nov.*; *Erigeron sionis* Cronq. var. *trilobatus* (Maguire) Welsh, *comb. nov.*; *Lygodesmia grandiflora* (Nutt.) T. & G. var. *doloresensis* (Tomb) Welsh, *comb. nov.*; *Lygodesmia grandiflora* (Nutt.) T. & G. var. *entrada* (Welsh & Goodrich) Welsh, *comb. nov.*; *Lepidium montanum* Nutt. var. *claronensis* Welsh, *var. nov.*; *Phacelia cronquistiana* Welsh, *sp. nov.*; *Phacelia pulchella* Gray var. *atwoodii* Welsh, *var. nov.*; *Astragalus toanus* Jones var. *scidulus* Welsh & Atwood, *var. nov.*; *Astragalus zionis* Jones var. *vigulus* Welsh, *var. nov.*; *Pediomelum aromaticum* (Payson) W. A. Weber var. *barnebyi* Welsh, *var. nov.*; *Trifolium friscanum* (Welsh) Welsh, *comb. nov.*; *Mentzelia goodrichii* Thorne & Welsh, *sp. nov.*; *Camissonia bairdii* Welsh, *sp. nov.*; *Camissonia claviformis* (Torr. & Frem.) Raven var. *cruciformis* (Kellogg) Welsh, *stat. nov.*; *Gilia latifolia* Wats. var. *imperialis* Welsh, *var. nov.*; *Eriogonum corymbosum* Wats. var. *albiflorum* (Reveal) Welsh, *comb. nov.*; *Eriogonum corymbosum* var. *atwoodii* (Reveal) Welsh, *comb. nov.*; *Eriogonum jamesii* Benth. var. *higginsii* Welsh, *var. nov.*; *Eriogonum racemosum* Nutt. var. *nobilis* Welsh & Atwood, *var. nov.*; *Aquilegia grahamii* Welsh & Goodrich, *sp. nov.*; *Penstemon franklinii* Welsh, *sp. nov.*; *Penstemon humilis* Nutt. var. *desereticus* Welsh, *var. nov.*; *Yucca vespertina* (McKelvey) Welsh, *comb. et stat. nov.*; *Allium geyeri* Wats. var. *chatterleyi* Welsh, *var. nov.*; *Spiranthes romanzoffiana* Cham. var. *diluvialis* (Sheviak) Welsh, *comb. nov.*


Key Words: New taxa, nomenclature, Utah flora

## INTRODUCTION

While undertaking a revision of *A Utah Flora* (Welsh et al., 1987) many previously unrecognized taxa were discovered and several nomenclatural combinations were found necessary. They are proposed as follows, with a complete treatment of the inclusive taxa where necessary. The state of Utah is large, diverse, and portions of it have yet to be investigated thoroughly from a bo-

tanical standpoint. Some of the taxa described below have resulted from investigations by several workers in previously poorly explored regions of the state, while others have been tucked away in the herbarium, placed within closely related entities. The second edition of *A Utah Flora*, now in press, will be more inclusive than previously because of the many new taxa reported here. The novelties and nomenclatural proposals included in that flora are validated in this work.

BORAGINACEAE

**Mertensia lanceolata** (Pursh) DC var. **coriacea** (A. Nels.) Higgins & Welsh, *comb. nov.* [based on: automatic tautonym created by publication of *M. coriacea* var. *dilatata* A. Nels., Bull. Torrey Club 29: 402. 1902].

This is a necessary nomenclatural adjustment to bring the name of the variety in line with contemporary rules of the International Code.

CARYOPHYLLACEAE

**Arenaria rubella** (Wahl) J. E. Sm. var. **filiorum** (Maguire) Welsh, *comb. nov.* [based on: *Arenaria filiorum* Maguire, Bull. Torrey Bot. Club 73: 326. 1946].

This combination recognizes the affinity of *A. filiorum* Maguire with the closely allied *A. rubella* (Wahl) J. E. Sm.

CHENOPODIACEAE

**Zuckia brandegei** (Gray) Welsh & Stutz var. **plummeri** (Stutz & Sanderson) Welsh, *comb. nov.* [based on: *Grayia brandegei* var. *plummerii* Stutz & Sanderson, Madrono 34: 148. 1987].

This combination recognizes the broad-leaves portion of *Zuckia brandegei* within the genus.

COMPOSITAE

**Agoseris glauca** (Pursh) Raf. var. **cronquistii** Welsh, *var. nov.* A *Agoseris glauca* var. *glauca* in foliis latioribus et integris,

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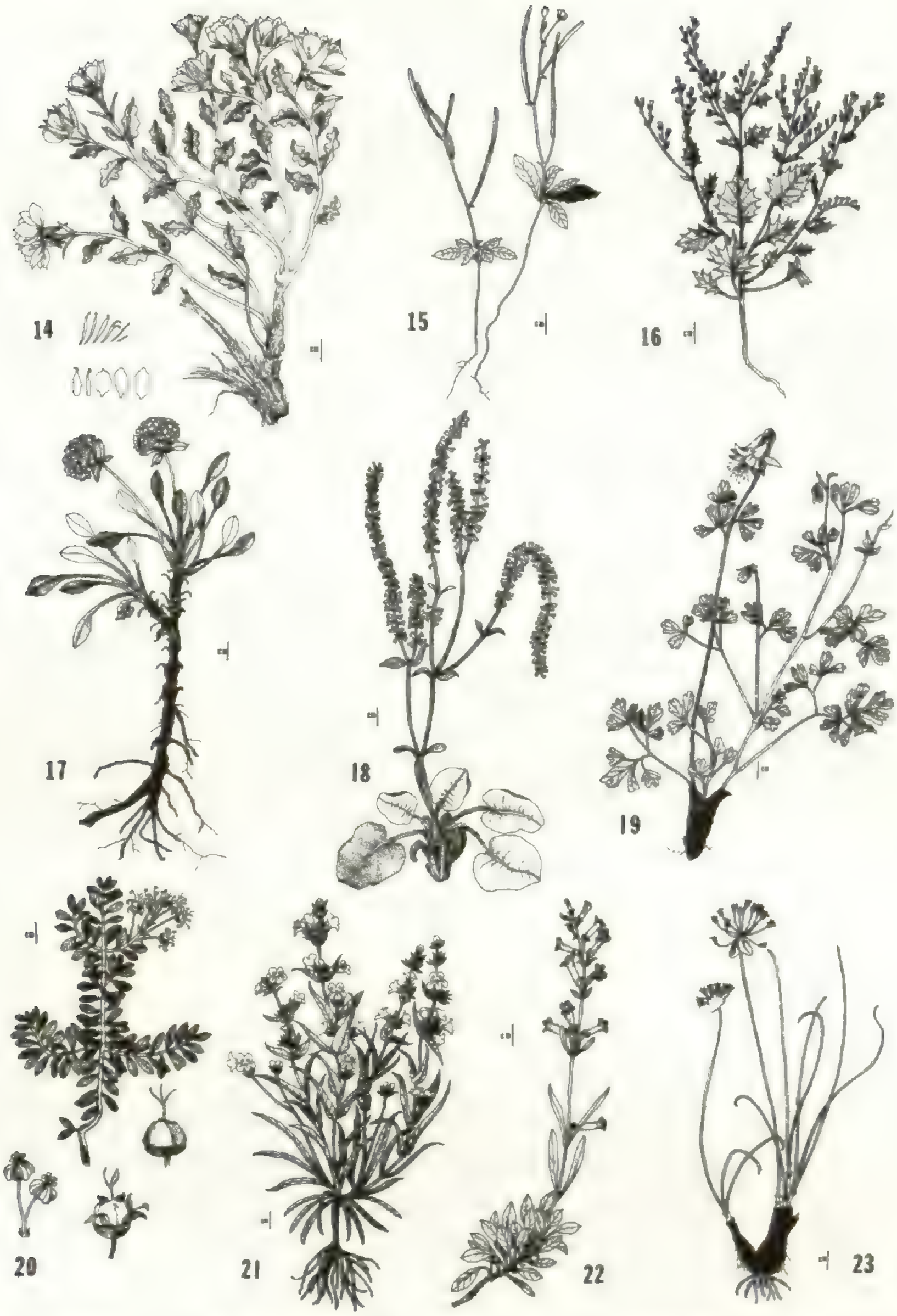


Figures 14–23. **14.** *Mentzelia goodrichii* Thorne & Welsh; **15.** *Camissonia bairdii* Welsh; **16.** *Gilia latifolia* Wats. var. *imperialis* Welsh; **17.** *Eriogonum jamesii* var. *higginsii* Welsh; **18.** *Eriogonum racemosum* Nutt. var. *nobilis* Welsh & Atwood; **19.** *Aquilegia grahamii* Welsh & Goodrich; **20.** *Ceanothus greggii* Gray var. *franklinii* Welsh; **21.** *Penstemon franklinii* Welsh; **22.** *Penstemon humilis* Nutt. var. *desereticus* Welsh; **23.** *Allium geyeri* Wats. var. *chatterleyi* Welsh.

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Figures 1–13. **1.** *Agoseris glauca* (Pursh) Raf. var. *cronquistii* Welsh; **2.** *Ambrosia sandersonii* Welsh; **3.** *Artemisia campestris* L. ssp. *borealis* (Pallas) H. & C. var. *petiolata* Welsh; **4.** *Haplopappus lignumviridis* Welsh; **5.** *Hymenoxys acaulis* (Pursh) Parker var. *nana* Welsh; **6.** *Senecio castoreus* Welsh; **7.** *Senecio musiniensis* Welsh. **8.** *Lepidium montanum* Nutt. var. *claronensis* Welsh; **9.** *Phacelia cronquistiana* Welsh; **10.** *Phacelia pulchella* Gray var. *atwoodii* Welsh; **11.** *Astragalus toanus* Jones var. *scidulus* Welsh & Atwood; **12.** *Astragalus zionis* Jones var. *vigulus* Welsh; **13.** *Pediomelum aromaticum* (Payson) W. A. Weber var. *barnebyi* Welsh.

statura inferiore, bracteis involucrorum purpureis lineatis vel omnes purpureis; scapis pubescentibus parce pubescentibus vel glabris differt, et in montibus excelsis crescens (Plate I: Figure 1).

TYPE: USA. **Utah.** Piute County, Tushar Mts., T27S, R5W, S35, at timberline, ca. 3050 m, 9 mi. due west of Marysvale, on silicious modified Tertiary volcanic gravel, 27 July 1976, *S. Welsh, K. Taylor, & D. Atwood 14021* (HOLOTYPE BRY!; one isotype previously distributed as *Agoseris glauca.*

ADDITIONAL SPECIMENS: **Utah.** Piute County. Head of Bullion Creek, ca. 9 mi. due WSW of Marysvale, 3050 m elev., 17 August 1978, *S. Welsh & J. Henriod 18170* (BRY!); head of Bullion Canyon, 28 July 1976, *S. Welsh, K. Taylor, & D. Atwood 14056* (BRY!); ca. 10 mi. WSW Marysvale, Belknap Mt., 3355 m, 27 July 1978, *S. Welsh, M. Welsh, J. Henriod 17887* (BRY!). Beaver County. Tushar Mts., Mt. Holly, 15 August 1984, *A. Taye 3124* (BRY!). Summit County. Bald Mountain, 27 July 1978, *K. Ostler & K. McKnight 1617* (BRY!); Bald Mountain Pass, 21 August 1984, *L. C. & E. Higgins 14785* (BRY!). San Juan County. La Sal Mts., between Mt. Peale and Mt. Melenthin, 3 August 1978, *N. D. Atwood 7087* (BRY!). Sanpete County. Ferron Mt., 10 August 1988, *D. Atwood & J. Tuhy 13441* (BRY!). Uintah County. Uinta Mts., SE of Marsh Peak, 19 August 1982, *S. Goodrich 17629* (BRY!). Duchesne County. Atwood Lake Basin, 15 July 1979, *S. Welsh, E. Neese, D. Atwood 19027* (BRY!).

This dwarf alpine phase of the species occurs at elevations of 3050 m and upwards. It is a dwarf plant, only seldom surpassing 18 cm in height. Scape apices vary from glabrous to tomentose, the leaves are ordinarily rather broadly elliptic to oblanceolate and typically entire (though rarely lobed), the involucres are glabrous, the bracts purplish throughout or with a broad median purple stripe. The plant is named to honor the memory of the late Dr. Arthur Cronquist, student of the genus and friend of plant taxonomy and taxonomists, who circumscribed the taxon in notes at BRY and in a manuscript for the impending treatment in the Intermountain Flora. He did not propose a formal name for the plant. Spruce-fir and alpine tundra communities at 3050 to 3660 m in the La Sal, Tushar, and Uinta mountains and on the Aquarius and Wasatch plateaus in Beaver, Daggett, Duchesne, Garfield, Piute (type from 9 mi. W of Marysvale), San Juan, Sanpete, Summit, and Uintah counties; endemic.

**Ambrosia sandersonii** Welsh, *sp. nov.* A *Ambrosia eriocentra* (Gray) Payne in foliis tenuis et bracteis glandularis nec pilosis longis differt (Plate 1: Figure 2).

TYPE: USA. **Utah.** Washington County, T43S, R19W, S16, Beaver Dam Well road, ca. .4 km up the wash, 4 April 1993, *S. Sanderson 93-02* (HOLOTYPE BRY!; ISOTYPES NY, GH, MO, US, POM, CAS, RM, UT, UTC).

ADDITIONAL SPECIMENS: **Utah.** Washington County, Beaver Dam Wash, Beaver Dam Well road, ca. .4 km up the wash, 4 April 1993, *S. Sanderson 93-01, 93-03, 03-04*; 14 April 1993, *S. Sanderson 93-05* (all BRY!).

Shrubs, mainly 5–8 dm tall; branchlets green, becoming straw-colored to ashy in age; herbage yellow green, puberulent; leaves 2–6 cm long, the main axis linear, 1.5–3 mm wide, pinnatifid with 1–5 acicular, irregularly spaced lateral lobes, or entire, white-tomentulose on both sides; staminate heads 2.5–4 mm high, 4.6–7.3 mm wide (when pressed), the bracts obtuse, ciliate, the margins not glandular; pistillate heads 7.3–8.8 mm high, all bracts chartaceous, glandular, the margins ciliate, with a midrib, spinulose apically. Blackbrush, creosote bush, and Joshua tree communities at ca. 825 m in Beaver Dam Wash, Washington County; endemic; 5 (0).

This plant simulates *Hymenoclea salsola* T. & G. in general appearance. Its slender leaves and habit of growth are very similar to that plant. Its herbage is puberulent as in *Ambrosia eriocentra* (Gray) Payne, however, not glabrous-glandular as in *Hymenoclea*, and the fruiting bracts are typical for an *Ambrosia*. The species is known from a few dozen individuals, which appears to be sustained by recruitment from viable seeds, not what would be expected if the plants were sterile hybrids. Indeed, the mature fruiting bracts appear to surround viable seed. The species is named after the collector, an excellent botanist and researcher who first recognized its affinities.

**Artemisia campestris** L. ssp. **borealis** (Pallas) H. & C. var. **petiolata** Welsh, *var. nov.* Plantis similis generaliter *Artemisia campestris* L. var. *scouleriana* (Benth.) Cronq. sed differente in petiolis caulis foliis brevioribus et foliis basalibus majoribus (Plate 1: Figure 3).

TYPE: USA. **Utah.** Duchesne County. T2N, R5W, S17, NW¼ USM, Ashley National Forest, Uinta Mts., trail between Little Meadow and Moon Lake, 2715 m elev., in ponderosa pine-lodgepole pine-manzanita community, 25 July 1984, *S. Goodrich 21096* (HOLOTYPE BRY!; 10 isotypes distributed previously as *Artemisia campestris* L.).

This variety differs from var. *scouleriana* by its long petioles, leaves with long, linear lateral lobes, and grayish pubescence. The

basal tuft of leaves is also much longer than for most Utah *A. campestris.*

**Erigeron sionis** Cronq. var. **trilobatus** (Maguire) Welsh, *comb. nov.* [based on: *Erigeron flagellaris* var. *trilobatus* Maguire ex Cronq., Brittonia 6: 258. 1947; *E. proselyticus* Nesom].

This combination is made necessary by recognition of the close affinity of the material from near Cedar Breaks, Iron County, with that of Zion Canyon.

**Haplopappus lignumviridis** Welsh, *sp. nov. Haplopappo crispi* L. Anderson Similis sed foliis non crispibus et capitulis parvioribus differt (Plate I: Figure 4).

TYPE: USA. **Utah.** Sevier County. T24S, R2W, S29 SW¼, SW¼, Cottonwood Creek riparian area, ca. 3 km S of Anabella, Utah, on moist tertiary igneous flows, with *Salix, Urtica gracilis,* and *Conyza canadensis,* 16 August 1983, *L. Greenwood 5566* (HOLOTYPE BRY!).

Shrubs ca. 3 dm tall or more, the branchlets smooth, resin-coated; leaves .7–2.8 cm long, 1.5–3 mm wide, entire, green, narrowly spatulate, acuminate, the apex spinulose, the margins smooth, resin-coated, not especially crowded below the inflorescence; heads 3–8 per branch, rather closely aggregated and cymose; involucres obconic, the heads 12–15 mm long, 4–8 mm wide when pressed; bracts in several series, resin-coated, none green or leaflike; rays ca. 5–8, 3–4 mm long; disk flowers ca. 8–12, pale yellow; pappus tawny; achenes ca. 5 mm long, rather densely hairy. Riparian area with willow, nettle, conyza, and other bottomland plants at ca. 1890 m in Sevier County; endemic; 1 (0).

This plant does not appear to be closely allied to any of the other shrubby species of *Haplopappus* in Utah.

**Hymenoxys acaulis** (Pursh) Parker var. **nana** Welsh, *var. nov.* Similis *Hymenoxys acaulis* var. *arizonica* (Greene) Parker. sed in habitu compactiore foliis brevioribus et scapis brevioribus differt (Plate I: Figure 5).

TYPE: USA. **Utah.** Emery County, T26S, R9E, S2, SW¼, ca. 3 mi. E of the Muddy River, San Rafael Reef; 1678 m elev., Morrison Formation, juniper-single leaf ash community, 6 May 1982, *D. Atwood & S. Goodrich 8652* (HOLOTYPE BRY; two isotypes distributed previously as *H. depressa*).

ADDITIONAL SPECIMENS: **Utah.** Emery County, T19S, R12E, S18, San Rafael Swell, Cedar Mountain summit, 2333 m elev., pinyon-juniper-ponderosa pine community, on Buckhorn Conglomerate, 18 May 1979, *J. Harris 126*; Red Canyon, east fork, ca. 8 km east of Buckhorn Wash, along San Rafael River, 5 June 1970, *S. L. Welsh & N. D. Atwood 9907*; Secret Mesa, San Rafael Swell, T22S, R9E, S25, ca. 1 mi. N of I-70, Navajo Sst, pinyon-juniper community, at 2100 m elev.; 24 May 1989, *S. L. Welsh & R. Kass 24303* (all BRY).

This taxon was previously included within *H. depressa,* which is a synonym of *H. torreyana.* Cronquist (personal communication) reviewed the material for the Intermountain Flora, and expanded the concept of the variety to include pulvinate caespitose phases herein regarded as portions of var. *lanata.* The dwarf plants regarded var. *nana,* seem to represent more than mere ecologically controlled variations; they apparently represent genetically controlled segregates in eastern Utah. Dwarf forms of *H. acaulis,* especially of the var. *lanata,* which have been mistaken for this entity, are more hairy and have usually broader leaves.

**Lygodesmia grandiflora** (Nutt.) T. & G. var. **doloresensis** (Tomb) Welsh, *comb. nov.* [based on: *Lygodesmia doloresensis* Tomb, Syst. Bot. Monogr. 1: 48. 1980].

This and the next bring into the fold of an expanded *L. grandiflora* all of the intergrading parts. All appear to have a common origin, with each of the constituent entities reflecting overlapping morphological characters that blend where geographical ranges overlap, which is considerable for most of the taxa.

**Lygodesmia grandiflora** (Nutt.) T. & G. var. **entrada** (Welsh & Goodrich) Welsh, *comb. nov.* [based on: *Lygodesmia entrada* Welsh & Goodrich, Great Basin Nat. 40: 83. 1980].

**Senecio castoreus** Welsh, *sp. nov.* Persimilis *Senecio werneriifolio* (Gray) Gray sed in capitulus eradiatis, foliis brevioribus, involucris majoribus differt (Plate I: Figure 6).

TYPE: USA. **Utah.** Beaver County. Tushar Mts., Mt. Belknap, T27S, R5W, S34, elev. 3538 m, in sparsely vegetated alpine tundra community, on a south-facing scree slope, 20 September 1987, *A. Taye 3680* (HOLOTYPE BRY; three isotypes distributed previously as *S. canus.*

ADDITIONAL SPECIMENS: **Utah.** Piute County, ca. 11 mi. W of Marysvale, Gold Mt., Tushar Mts., Fish Lake National Forest, T27S, R5W, S35, 18 July 1981, *N. D. Atwood 8025*; T27S, R5W, S26, Tushar Mts., Gold Mt., 14 August 1984, *A.*

*Tayle, N. D. Atwood, & S. Goodrich 3092*; Tushar Mts., ridge crest ca. 1 km ESE of Mt. Belknap summit, T27S, R5W, S35, 20 September 1987, *A. Taye 3667*; T27S, R5W, S34, SW¼, SW ridge of Mt. Belknap, ca. 10 mi. WSW of Marysvale, 21 July 1984, *J. S. Tuhy & K. Johnson 1704*; Tushar Mts., ridge crest ca. .5 km SE of Mt. Belknap summit, T27S, R5W, S34, 20 September 1987, *A. Taye 3674*; T27S, R5W, S26, N½, Gold Mt., Tushar Mts., 28 August 1991, *R. Kass 3320* (all BRY).

Perennial herbs, typically with a subterranean caudex, sometimes somewhat soboliferous; plants 7–16 cm tall, erect or ascending; herbage more or less woolly-tomentose; basal leaves petiolate, the blades 1–1.5 cm long, 5–10 mm wide, oval to oblanceolate or oblong, entire or denticulate apically, obtuse to rounded apically; main lower cauline leaves the largest, with oval to obovate or oblanceolate blades 1.2–3.2 mm long, these entire, somewhat toothed or rarely pinnatifid, the upper ones often clasping, finally bracteate; heads mainly 1–5, subumbellately corymbose; involucres 6–9 mm long, 7–13 mm wide when pressed; main bracts 13–10, lance-attenuate, suffused with purple throughout or only at the tips or bases, typically somewhat tomentose; outer bracts very short; rays lacking; achenes glabrous. Polemonium, trisetum, festuca, and arenaria communities, often on windswept ridges or less commonly downward to the spruce-fir community, in thermally modified Tertiary igneous outcrops and gravels, at 3355 to 3875 m in Beaver and Piute counties; endemic.

Besides differing from *S. canus* in lacking ray flowers, this plant has involucres that average larger, and has shorter basal leaves. It is a true alpine dwarf, growing at very high elevations in the Tushar Mountains, which are known locally as the Beaver Mountains.

**Senecio musiniensis** Welsh, *sp. nov.* Similente *Senecio fendleri* Gray sed in involucris majoribus staturis parvioribus et sobolibus consinstentibus differt, sed affini plus arcte ad *S. canus* Hook. et *S. multilobatus* T. & G, e qua in sobolibus nullus et corollis radiis prominentibus id differt (Plate I: Figure 7).

TYPE: USA. **Utah.** Sanpete County. Ferron Mountain, above Ferron Reservoir, T19½S, R5E, S31, NW¼, on steep south-facing slope, on white Flagstaff Limestone, at 3218 m elev., 1 August 1988, *N. D. Atwood & J. Tuhy 13438*; (HOLOTYPE BRY; 7 isotypes distributed previously as *Senecio canus*).

ADDITIONAL SPECIMENS: **Utah.** Sanpete County, Camal Rock area, head of Twelve-

mile Creek, broken limestone area, Flagstaff, 23 July 1976, *M. E. Lewis 4274*; Ridge to Musinea Peak, 18 July 1978, *M. E. Lewis 5516* (both BRY).

Perennial soboliferous herbs, with stems of the season arising from sobol apices; plants mainly 5–10 cm tall, erect or ascending; herbage appearing gray due to a dense floccose-tomentose; basal leaves petiolate, the blades 1–2.5 cm long, 4–10 mm wide, pinnatifid or pinnately lobed; largest cauline leaves above the base, only somewhat reduced upward, becoming sessile and finally bracteate; heads 3 to many, corymbose; involucres 8–9 mm high, 4–8 mm wide when pressed; main bracts 8–12, oblanceolate to oblong, rather abruptly acute, yellow-green to purple or with a purplish midstripe and apex, the margins scarious or hyaline, sparingly tomentose to glabrous; outer bracts very short; ray flowers lacking, or occasionally 1 per head, when present yellow and ca. 6 mm long; pappus white; achenes glabrous; $n = 23$. Ridge tops on Flagstaff Limestone barrens and talus slopes at Musinea Peak and on margins of the Wasatch Plateau, at ca. 2960 to 3295 m in Sanpete County; endemic.

This taxon appears to be allied to *S. canus* (source of gray tomentum) and *S. multilobatus* (source of the pinnatifid leaves); it differs from both in the presence of sobols and in the eradiate or only sparingly radiate heads.

### CRUCIFERAE

**Lepidium montanum** var. **claronensis** Welsh, *var. nov.* A *Lepidio montano* Nutt. var. *montano* in habitus perenni et inflorescentia frondoso caule longiore differt (Plate I: Figure 8).

TYPE: USA. **Utah.** Garfield County, T35S, R4½W, SW/NW S10, Casto Canyon, Dixie National Forest, in scattered ponderosa pine with Apache plume, on SW exposure, at ca. 2196 m, 14 June 1990, *N. D. Atwood, B. Franklin, & B. Reynolds 13744* (HOLOTYPE BRY!).

ADDITIONAL SPECIMENS: **Utah.** Garfield County, T31S, R2W, S26, ca. 5 km S of Antimony, along the Sevier River, at ca. 2013 m, 4 June 1984, *L. C. Higgins et al. 14271*; T31S, R1W, S6, near mouth of Dry Wash, 20 Sept. 1992, *K. T. Anderson 552*. Kane County; ca. 6 km E of Hwy 89 on road to Alton, T39S, R6W, in ponderosa community, 25 June 1983, *N. D. Atwood 9471*. Piute County; Dry Fork Canyon, ca. 8 km NE of Antimony, T30S, R1W, S32, 28 July 1976, *S. L. Welsh et al. 14124* (all BRY!).

This is a dwarf perennial with marcescent leaf bases on the caudex branches. It shares its perennial habit with both var. *nee-*

*seae* Welsh & Reveal and var. *stellae* Welsh and Reveal; from the former the plants differ in having pinnatifid basal and cauline leaves and from the latter in having glabrous pods. The plant occurs in montane habitats and has about the same morphological and geographic integrity as do other varieties in the species.

## HYDROPHYLLACEAE

**Phacelia cronquistiana** Welsh, *sp. nov.* Persimilis *Phacelia incana* Brand sed in calyce ad anthesis bereviore planta parviore, pilis glandulosis brevioribus et seminibus parvioribus differt (Plate I: Figure 9).

TYPE: USA. **Utah.** Kane County: T40S, R4½W, head of Johnson Canyon, 4.5 km E of junction on road to Cannonville, at 1920 m, on clay outcrops in pinyon-juniper-sage community, 13 June 1983, *N. D. Atwood 9458* (HOLOTYPE BRY!; isotypes, none distributed previously as *Phacelia incana*.

ADDITIONAL SPECIMENS: **Utah.** Kane County, 4.5 km E of Skutumpah-Alton Junction, at head of Johnson Canyon, T40S, R4½W, 7 June 1969, *N. D. Atwood 1800, 1803*; 4.5 km E of Hwy 89, on road to Alton, T32S, R6W, ponderosa pine community at ca. 2100 m, 25 June 1983, *N. D. Atwood 9472* (all BRY!).

Annual, 6–9 (10) cm tall; stems erect, shortly capitate-glandular, simple or branching from the base; leaves essentially all cauline, petiolate, the blades 3–7 mm long, 2–6 mm wide, oval to rhombic, often broader than long, entire or less commonly some crenate; cymes terminal on main stems and branches, 2–6 cm long in fruit; pedicels ca. .5 mm long at anthesis, becoming up to 4 mm long in fruit; sepals linear-oblong to spatulate, 2–2.8 (3.2) mm long at anthesis, to 6; .2 mm long in fruit, .5–1.2 mm wide; corolla tubular-campanulate, 3.5–4 mm long, pale purple with a white tube; anthers included; style bilobed; seeds ca. 25–35, ca. .3–.4 mm long, pitted. Pinyon-juniper-sagebrush and ponderosa pine communities at 1920 to 2100 m in western Kane County; endemic.

This taxon is dedicated to the late Dr. Arthur Cronquist, who first noted it as distinctive. The plant was initially collected by N. D. Atwood in 1969 and identified as *P. rotundifolia* Torr. ex Wats., and later as both *P. pulchella* Gray and *P. lemmonii* Gray. It is most similar to *P. incana,* however, differing in its shorter flowering calyx, smaller size of all parts, shorter glandular pubescence, and smaller seeds. Similar, and perhaps identical material was collected in 1993 by N. D. Atwood from near Mt. Trumbull in Arizona.

**Phacelia pulchella** Gray var. **atwoodii** Welsh, *var. nov.* Similis *Phacelia pulchella* Gray var. *pulchella* in floribus coloris et magnitudine sed in foliis crenatis consistantibus differt et var. *sabulonum* in foliis crenatis sed in corollis magnitudine et foliis tenuissimis texturis differt (Plate I: Figure 10).

TYPE: USA. **Utah.** Kane County: T43S, R4W, S33, S of Hwy 89, ca. 10 km E of Johnson Canyon, Moenkopi Formation, juniper-sagebrush community, 24 April 1992, *S. L. Welsh & K. H. Thorne 24900* (HOLOTYPE BRY; 9 isotypes to be distributed).

ADDITIONAL SPECIMENS: **Utah.** Kane County: T44S, R5S, S1, 10 May 1992, *K. Thorne & C. Zupan 10125*; T43S, R2W, S30, Cockscomb, south road, Carmel Formation, 8 May 1992, *K. Thorne & C. Zupan 10073*; T43S, R4W, S33, S of Hwy 89, ca. 10 km E of Johnson Canyon, 29 May 1992, *S. L. Welsh 25037*; ca. 32 km E of Hwy 89, along Alton Road, T40S, R5W, 25 June 1989, *N. D. Atwood 9470.*

Pinyon-juniper, oak, sagebrush, single-leaf ash, and service-berry communities at ca. 1550 to 1680 m in western Kane County; endemic. This is the pretty annual phacelia that grows with other plants in the duff that accumulates in the shelter of juniper trees and other desert shrubs in western Kane County.

LEGUMINOSAE

**Astragalus toanus** Jones var. **scidulus** Welsh & Atwood, *var. nov.* A *Astragalo toano* Jones in floribus minoribus et pallidioribus et leguminibus latioribus differt (Plate I: Figure 11).

TYPE: USA. **Arizona.** Mohave County: T37N, R10W, S33, Mohave Strip, E flank of Diamond Butte, with mixed juniper-eriogonum-hilaria community, on Moenkopi Formation, at ca. 1600 m elev., 16 April 1989, *N. D. Atwood & S. L. Welsh 13526* (HOLOTYPE BRY!; ISOTYPES NY, GH, MO, US, POM).

ADDITIONAL SPECIMENS: **Arizona.** Mohave County: T37N, R10W, S33, Mohave Strip, E. flank of Diamond Butte, 20 May 1987, *N. D. Atwood & K. H. Thorne 12691* (BRY!).

This phase of *A. toanus* is disjunct from the main distribution of the species by more than 150 km, and while it differs only in degree from the species, it is most certainly isolated, reducing the possibility of genetic exchange to essentially zero. The flowers average smaller than for the species as a whole, are pale throughout, a greenish yellow or dull whitish, but with pure white wing-tips as in the species. The pods are broader than for the bulk of the *A. toanus* specimens examined, being approached in width by only a few specimens.

**Astragalus zionis** Jones var. **vigulus** Welsh, *var. nov.* Similis *Astragalo zionis* var. *zionis* sed in leguminibus longioribus et latioribus differt (Plate I: Figure 12).

TYPE: USA. **Utah.** Washington County. T39S, R13W, S20, along side the Browse road to Guard station, E side of the Pine Valley Mts., at 2000 m elev., sandy soil, in pinyon-juniper-mountain brush community, 7 June 1983, *L. C. Higgins 13577* (HOLOTYPE BRY!; four isotypes distributed previously as *A. tephrodes* Gray).

ADDITIONAL SPECIMENS: **Utah.** Washington County, T39S, R14W, S28, Pine Valley Mountains north slope, 2500 m elev., 23 June 1983, *L. C. Higgins 13769*; T39S, R13W, S30, ca. 5.5 mi N of I-15 on Browse turnoff to Harmon Creek, 8 June 1981, *N. D. Atwood 7893*; T39S, R13W, E slope of Pine Valley Mts., between Browse guard station & Syler Spring, 16 May 1984, *N. D. Atwood 9556*; T39S, R13W, S30, ca. 7 mi. W of Browse Interchange, oak-Garrya community, 22 April 1982, *S. L. Welsh & N. D. Atwood 21056*; T39S, R13W, S30, Jct Blake-Harmony trail and Browse road, 19 May 1986, *R. B. & D. R. Warrick 1421* (all BRY!).

Specimens of this taxon have very coarse, large pods and grow in huge mats or clumps to a meter wide or more. It was mistaken previously as a phase of *A. tephrodes* Gray, which is still unknown in the state. It grows in pinyon-juniper and mountain brush communities on the east and north flanks of the Pine Valley Mountains in Utah.

**Pediomelum aromaticum** (Payson) W. A. Weber var. **barnebyi** Welsh, *var. nov.* Persimilis *Pediomelo aromatico* (Payson) W. A. Weber var. *aromatico* sed in inflorecentiis infimis per multifloris (10-12 nec 3-7) et pedunculis longioribus (.7–1.3 nec .1–.5 cm) differt (Plate I: Figure 13).

TYPE: USA. **Utah.** Washington County, Hilldale, T43S, R10W, S26, ca. 1350 m elev., in pinyon-juniper forest, Chinle Formation, 3 June 1993, *S. L. Welsh & K. H. Thorne 25586* (HOLOTYPE BRY!; ISOTYPES, NY, GH, MO, US, POM, CAS, RM, UT, UTC, and others).

ADDITIONAL SPECIMENS: **Arizona.** Mohave County, on red sandstone with pinyon-juniper and *Shepherdia rotundifolia,* 1560 m in the canyon N of Colorado City. Widely rhizomatous (no tuber); banner purplish fading whitish; wings purple-tipped, 10 May 1986, *R. C. Barneby 18129* (BRY!; NY?). Ca. 8 km north of Moccasin, on Coral Pink sand dunes road, on Chinle Formation, 19 May 1972, *N. D. Atwood & L. C. Higgins 3935* (BRY!). **Utah.** Washington County, near base of Canaan Mountain, north of Colorado City, elev. 1373–1525 m. Navajo sandstone formation, 14 May 1991, *L. M. Shultz/J. Anderson 5385* (NY; UTC?).

Pinyon-juniper and silver buffaloberry community at ca. 1560 m on Navajo Sandstone adjacent to Short Creek, north of Colorado City, Mohave County, Arizona and immediately contig-

uous Hilldale, Washington County, Utah, and eastward evidently on the Chinle Formation north of Moccasin.

The locally abundant, widely rhizomatous and hence colonial, plants grow in patches at the southern base of Canaan Mountain near Short Creek and eastward below of the Pink Cliffs to the vicinity of Moccasin, in at least two slightly disjunct populations far removed from the nearest populations of the species, which otherwise is known only from eastern Utah and adjacent Colorado. Their morphological discontinuities are in the order of magnitude of varietal segregants in this and other genera. More specimens might demonstrate even more substantial diagnostic characters. It seems certain that there is little possibility for genetic interchange between the disparate populations.

The distribution of Barneby's pediomelum is almost matched by that of the totally unrelated *Cycladenia humilis* Gray, which occurs in disjunct populations on seleniferous siltstone formations, including the Chinle, from the base of the La Sal Mountains in Colorado and Utah disjunctly to Chinle Formation west of Moccasin in Mohave County, Arizona. Both the *Cycladenia* and the *Pediomelum* are to be expected at other locations on the Chinle (and possibly on the Moenkopi) where it outcrops in Mohave and Kane counties. A solitary specimen of this species (*Atwood and Higgins 3935,* cited above), in vegetative condition has long been troublesome among the herbarium specimens of this genus from the vicinity of the Arizona Strip and adjacent Kane and Washington counties, where there exists a series of species within this distinctive genus. That specimen was initially placed with the poorly understood *P. epipsilum,* but always stood out because of the attenuate (not foliose) stipules and densely white hairy, very elongate (not short, mostly obscured) internodes. The taxon was subsequently found by Shultz and Anderson, and by Dr. Barneby, in the Short Creek area about 30 km west of the initial discovery. The habitat seems to be confined mainly to the Chinle silts and muds, in spite of other formations being designated on the collection labels. The Chinle is immediately overlain by sandstones older than the Navajo, but resembling that formation. The *P. aromaticum* complex extends from the vicinity of the La Sal Mountains in both Colorado and Utah into San Juan County, and disjunctly southwestward to the vicinity of Canaan Mountain in Washington County, Utah and Mohave County, Arizona. The segregates can be distinguished by the following key.

1. Lowermost racemes, at least, (7) 8- to 12-flowered and on peduncles .7–1.3 cm long; plants of Short Creek vicinity, Washington County and adjacent Mohave County, Arizona *P. aromaticum* var. *barnebyi*
– Lowermost racemes mainly 3- to 7-flowered and on peduncles less than .5 cm long; plants of eastern Utah and adjacent Colorado 2

2(1). Stems prostrate-ascending; flowers mainly 7–9 mm long; plants of rimrock and shallow sand in San Juan County *P. aromaticum* var. *tuhyi*
– Stems mainly erect or ascending; flowers mostly 10–12 mm long; plants of Emery(?) and Grand counties *P. aromaticum* var. *aromaticum*

Var. *aromaticum* Pinyon-juniper and mixed desert shrub communities at ca. 1530 m in Emery (?) and Grand counties; Paradox Basin, Colorado; essentially a Navajo Basin endemic.

Var. *barnebyi* Welsh Pinyon-juniper and silver buffaloberry community at ca. 1560 m on Navajo Sandstone adjacent to Short Creek, north of Colorado City, Washington County, Utah and immediately adjacent Mohave County, Arizona east to the vicinity of Moccasin.

This plant is far removed from the nearest populations of the species, which otherwise is known only from eastern Utah and adjacent Colorado. Its differences are in the order of magnitude of varietal differences in this and other genera. More specimens might demonstrate even more substantial characters than those cited in the key.

Var. *tuhyi* Welsh Pinyon-juniper and mixed desert shrub communities on the Entrada, Kayenta, and Mossback formations, Rone Bailey Mesa (type locality, *Welsh & Neese 23500,* 1985, HOLOTYPE BRY!), Canyonlands overlook, and Six-shooter Peak vicinities, on rimrock or shallow sand, at 1700 to 1985 m in San Juan County; endemic.

This variety has been discounted by recent workers in the genus. It does, however, demonstrate more than a mere trend in variation—the plants are isolated from the main body of the species to the north and east, and the flowers are consistently smaller. Even though occasional specimens in the type variety have flowers approaching the size of those in this variety, they are generally

larger. And, the prostrate-ascending stems of var. *tuhyi* are not due to the plants growing on unstable slopes. Quite the contrary is true; the substrates are quite stable, often the plants grow with roots in crevices in bedrock.

**Trifolium friscanum** (Welsh) Welsh, *comb. nov.* [based on: *Trifolium andersonii* var. *friscanum* Welsh, Great Basin Naturalist 38: 355. 1968].

This taxon is distinguished clearly from *T. andersonii* Gray, by its 3 (not 4 or 5) leaflets, short free tips of stipules, short petioles and few-flowered racemes. Furthermore, the plant is more than 250 km distant from the nearest known locality for *T. andersonii.*

LOASACEAE

**Mentzelia goodrichii** Thorne & Welsh, *sp. nov.* Similis *Mentzelia multicaulis* (Osterh.) Goodman in duratione, aspectu, et caudice sed in petalis majoribus et plus numerosis (10 nec 5) et foliis majoribus insigniter divergente (Plate I: Figure 14).

TYPE: USA. **Utah.** Duchesne County. T11S, R12E, NE¼ S5, West Tavaputs Plateau, Badland Cliffs, breaks north of Argyle Canyon, at 2623 to 2684 m, with scattered bristlecone pine, on marl limestone, on steep south exposure, 15 July 1992, *C. Goodrich 23806* (HOLOTYPE BRY!; ISOTYPES NY, GH, MO, US, POM, CAS, RM, UT, UTC, and others).

ADDITIONAL SPECIMENS: **Utah.** Duchesne County: T11S, R13E, S6, East Tavaputs Plateau, Badland Cliffs, escarpment at rim of Argyle Canyon, scattered limber pine, pinyon, Douglas fir, holodiscus, on Green River Formation, on 60 to 80% southern exposure, 6 July 1992, *S. Goodrich 23781* (BRY!; 11 duplicates to be distributed); T6S, R8W, S4, Upper NE slope of Willow Canyon, south facing slope of white shale, 3 July 1988, *M. A. Franklin & J. Chandler 6258* (BRY!; 5 duplicates distributed previously as *M. multicaulis*).

Long-lived, clump-forming perennial, of shaly slopes, from a branching woody caudex and stout taproot; stems white, puberulent, diffusely branched from near the base, flexuous, the branches initially widely spreading, becoming curved-ascending; leaves narrowly oblong to narrowly oblanceolate or lanceolate in outline, shallowly undulate-dentate with few rounded to obtuse teeth on each side; some of the upper leaves and bracts entire, linear to linear-lanceolate; ultimate branches of inflorescence 1- to

3-flowered; calyx lobes 8–13 mm long; petals 10, oblanceolate; 12–20 mm, 5–10 mm wide; outer petaloid stamens spatulate, narrower and shorter than the petals; capsule 12–13 mm long, cylindric; seeds immature, whitish, evidently winged. Steep, white, marly calciferous shale outcrops of Green River Formation with scattered limber pine, pinyon pine, Douglas fir, mountain mahogany, and rabbitbrush, along escarpment of Willow and Argyle canyons, at 2470 to 2685 m, in Duchesne County; endemic.

This plant has the general branching pattern of *M. multicaulis,* which also has a well developed though superficial caudex. It is likewise similar to that entity in bearing mainly cauline leaves, but it differs significantly in having ten large petals, a subterranean caudex, and in the larger green leaves.

## ONAGRACEAE

**Camissonia bairdii** Welsh, *sp. nov.* Plantis similis *Camissonia scapoidea* (Torr. & Gray) Raven sed in capsulis longioribus et glandulari-pubescentibus ubique differt (Plate I: Figure 15).

TYPE: USA. **Utah.** Washington County. T40S, R17W, SW¼ S19, between Manganese Wash and Miner's Canyon, ca. 3 km E of Gunlock, pinyon-juniper community, in clay soil of Carmel Formation, 11 May 1987, *G. I. Baird & M. A. Franklin 2657* (HOLOTYPE BRY!; two isotypes distributed previously as *Camissonia*).

ADDITIONAL SPECIMENS: **Utah.** Washington County. Along dirt road south of Rockville and at the west base of Smithsonian Butte, 26 May 1973, *N. D. Atwood 5139*; T40S, R17W, SW S19, ca. 3 km E of Gunlock, between Manganese Wash and Miner's Wash, in blackbrush community, 11 May 1987, *M. A. (Ben) Franklin & G. Baird 4700A*; Petrified Forest, head of Huber Wash, T41S, R11W, S25, north of Rockville, 4 May 1989, *S. L. Welsh & S. L. Clark 24281* (all BRY!).

Annual herbs from taproots; stems mainly 4.5–12 cm tall, simple, with main foliage leaves near the stem base; herbage minutely glandular puberulent, and sometimes also sparingly villous with long hairs; leaves petiolate, the blades simple (or with one to few, tiny, lateral segments), .8–3 cm long, 5–13 mm wide, lance-ovate to lanceolate, subentire to undulate-crenate; flowers 2–6, in terminal, minutely bracteate, nodding, subscapose racemes; hypanthium 1–1.8 mm long; sepals 3.3–4 mm long, reflexed at anthesis; petals yellow, often red–spotted near the base, 4–5 mm long; stamens 8, dimorphic, the longer usually surpassing the shorter by ca. 1 mm; anthers 1–1.9 mm long; pedicels ascending, 3–14 mm long; capsules 33–50 mm long, 1.8–2.2 mm thick; seeds in

2 rows per locule, ca. 1 mm long, not winged. Blackbrush and pinyon-juniper communities at ca. 1190 to 1310 m in Washington County; endemic.

Specimens of this plant have been variously identified, an indication that they did not readily fit into any of the known species. They are apparently most closely allied to *C. scapoidea,* however, the long pods simulate those of *C. chamaenerioides* but are much thicker. And the rather uniform glandular puberulence coupled with geographic disjunction from *C. scapoidea* lends credence to the designation of the material as belonging to a different taxon.

**Camissonia claviformis** (Torr. & Frem.) Raven var. **cruciformis** (Kellogg) Welsh, *stat. nov.* [based on: *Oenothera cruciformis* Kellogg, Proc. Calif. Acad. Sci. 2: 227. 1873].

A solitary specimen (*Baird 1964-b* BRY!), possibly belonging to this taxon, is known from Beaver Dam Wash, Washington County, Utah. If correctly identified it is far removed from the remainder of the variety in western Nevada and southern Oregon.

## POLEMONIACEAE

Specimens of *Gilia latifolia* Wats. were discovered in 1971 in Warm Creek Canyon, north of Lake Powell in Kane County. Since then the species has been found growing in Cataract Canyon, in the vicinity of Big Drop rapids and Imperial Canyon, in both Garfield and San Juan counties. It was also discovered in the San Rafael Swell vicinity in southern Emery and adjacent Wayne counties. These eastern materials have somewhat smaller floral and fruiting parts, more confluent leaves, and more intricately branched inflorescences than do those from the body of the species to the west. They are geographically isolated from plants of the type variety far to the west, and are distinguished as follows:

**Gilia latifolia** Wats. var. **imperialis** Welsh, *var. nov.* Similis var. *latifolia* in foliis latioribus et habitis generalis, sed in calycis, calycis dentibus, et capsulis minoribus, foliis plus confluentibus, et plantis majoribus differt (Plate I: Figure 16).

TYPE: USA. **Utah.** San Juan County, T31S, R17E, S33, Cataract Canyon, ca. .8 km N of Imperial Canyon, at ca. 1129 m, in mixed desert shrub community on Hermosa Formation, 15 Sept. 1983, *S. L. Welsh 22507* (HOLOTYPE BRY!; four isotypes previously distributed as *Gilia latifolia* Wats.).

ADDITIONAL SPECIMENS: **Utah.** Emery County, T26S, R9E, S32, San Rafael Swell, Maroni Slopes, 5 June 1980, *J. G. Harris 874* (BRY!). Garfield County, T31S, R17E, S15, Big Drop, Cataract Canyon, 5 May 1983, *S. L. Welsh 21819* (BRY!). Kane County, Warm Creek Canyon, 1.5 km S of access road, in sandy wash bottoms, 18 June 1971, *N. D. Atwood/R. Allen 2901* (BRY!); Tibbet Canyon, ca. 24 km NE of Glen Canyon City, Straight Cliffs Formation, 4 September 1973, *N. D. Atwood 5959* (BRY!). San Juan County, T31S, R17E, S17, Big Drop Two rapids, Colorado River, Cataract Canyon, 14 October 1983, *S. L. Welsh 22649* (BRY!); T31S, R17E, S33, Cataract Canyon, Imperial Canyon, 20 September 1983, *S. L. Welsh & E. Neese 22534* (BRY!); T31S, R17E, S21, Big Drop Three, 8 August 1983, *L. C. Higgins et al. s.n.* (BRY).

This gilia can be distinguished from the typical western material by the following key:

1. Calyx 2.8–4.8 mm long, the teeth 1–2 mm long; capsules 3–4.5 (4.9) mm long; plants often over 2.5 dm tall, known from Emery, Garfield, Kane, and San Juan counties *G. latifolia* var. *imperialis*
– Calyx (4.4) 5–6.9 mm long, the teeth 2–3.6 mm long; capsules (4.5) 5.2–7 mm long; plants mainly less than 2.5 dm tall, known from Washington County *G. latifolia* var. *latifolia*

Var. **imperialis** Welsh Shadscale and other mixed desert shrub communities at 1160 to 1590 m in Emery (Moroni Slopes, San Rafael Swell), Garfield, Kane, San Juan, and Wayne counties (where they abut on Cataract Canyon); endemic. The plants are locally common in Cataract Canyon, where they occur among boulders above high water level in a salt-desert shrub community. Its disjunct distribution is a near match for that of *Opuntia basilaris* Engelm. & Bigel var. *heilii* Welsh & Neese.

Var. **latifolia** Creosote bush and blackbrush communities at ca. 825 m in Washington (type from near St. George) County; California, Arizona, and Nevada. The type of the species was collected by C. C. Parry in 1874 near St. George, but the species has been taken again in Utah only rarely. It is locally common in desert tracts in southern Nevada and California.

## POLYGONACEAE

**Eriogonum corymbosum** Benth. var. **albiflorum** (Reveal) Welsh, *comb. nov.* [based on: *Eriogonum thompsonae* Wats. var. *albiflorum* Reveal, Madrono 19: 299. 1968].

The alliance of *E. thompsonae* sens. lat. with *E. corymbosum* appears to be inevitable, due to mixing of characters, especially in Washington County, where the types of var. *aureum* typically assigned to *E. corymbosum* and varieties *matthewsiae* and *albiflorum* were taken. The combination of *thompsonae* with *corymbosum* allows for solution of the problem of what to do with the many intermediates, which indicate a close relationship of the two complexes. Hence, the need for formal proposal of the combinations contained herein.

The transitionally narrow-leaved counterpart of var. *albiflorum* in Mohave County, Arizona, is recognized as *E. corymbosum* Benth. var. **atwoodii** (Reveal) Welsh, *comb. nov.* [based on: *Eriogonum thompsonae* Wats. var. *atwoodii* Reveal, Great Basin Nat. 34: 245. 1974].

**Eriogonum corymbosum** Benth. var. **thompsonae** (Wats.) Welsh, *comb. nov.* [based on: *Eriogonum thompsonae* Wats., Amer. Nat. 7: 302. 1873].

This taxon, with its subacaulescent habit, smooth yellow green leaves, and bright yellow flowers is an attractive plant on the Chinle muds and silts from the vicinity of Kanab westward to Colorado City. It is transitional in every way with both varieties *albiflorum* and *atwoodii.* Additionally in passes through var. *albiflorum* to the *E. corymbosum* varieties *matthewsiae* Reveal and *aureum* Jones.

**Eriogonum jamesii** Benth. var. **higginsii** Welsh, *var. nov.* Similis *Eriogono jamesii* Benth. var. *flavescens* in coloris florum et habitu, sed in monoinvolucris differt (Plate I: Figure 17).

TYPE: USA. **Utah.** San Juan County, T34S, R25E, S3, ca. 0.5 mi. W of junction to Eastland on Hwy 666, sagebrush community, in sandy soil, 19 June 1985, *L. & E. Higgins 15823* (HOLOTYPE BRY!; 8 isotypes distributed previously as *E. jamesii* var. *flavescens* Wats.

ADDITIONAL SPECIMENS: **Utah.** San Juan County, Junction of Hwy 160 and the road to Eastland; sandy soil; pinyon-juniper-artemisia community, 3 July 1970, *L. C. Higgins 3567* (BRY!); along Hwy 160, 11.3 mi. E of Monticello on low flats and rolling hills, associated with sagebrush, in large mats to 6 dm across, 28 June 1971, *J. L. Reveal 2502* (BRY!).

The plants from San Juan County are far removed geographically from the remainder of the species in Utah. The specimens

examined, all from about the same locality, have uniformly monoinvolucrate inflorescences, a condition that occurs occasionally within the distribution of the allied var. *flavescens*. However, that condition is seldom correlated on a population basis, and although admittedly a weakly disposed taxonomic character, the plants are readily identifiable.

**Eriogonum racemosum** Nutt. var. **nobilis** Welsh & Atwood, *var. nov.* Similis var. *zione* in caulibus leviter fistulosis et var. *racemoso* in habitu generali sed e ambo in floribus pallidis flavescentibus differt (Plate I: Figure 18).

TYPE: USA. **Utah.** San Juan County, T40S, R21E, S33, along the San Juan River, ca. 3 mi. W of Bluff, sandy soil, in atriplex/populus comm., at ca. 1300 m elev., 10 Sept. 1991, *N. D. & J. Atwood 17250* (HOLOTYPE BRY; ISOTYPES NY, US, MO).

This is a tall, slender phase of the species with numerous involucres in the inflorescence and cream to yellowish flowers. It is disjunct from the similar var. *zionis* by more than 150 km.

## RANUNCULACEAE

**Aquilegia grahamii** Welsh & Goodrich, *sp. nov.* A *Aquilegia micrantha* Eastw. in floribus rubro-purpureis et luteis, a *A. formosa* Fisch. ex DC. in glandiferis omnino et var. *fosteri* in petalis brevioribus et floribus longioribus, et a *A. flavescens* var. *rubicundula* (Tidestr.) Welsh in floribus atrorubropurpureus et longioribus quam latioribus differt (Plate I: Figure 19).

TYPE: USA. **Utah.** Uintah County, T2S, R22E, SW¼ S7, Hole In The Wall Canyon, 10 mi. 14°N of Vernal, Uinta Mountains, Ashley National Forest, sandy soil along drip line below weeping, haning garden cliffs of Weber Sandstone, growing with *Calamagrostis scopulorum,* at ca. 2320 m, 21 June 1993, *A.Huber & C. Plunkett 91* (HOLOTYPE BRY!; ISOTYPES NY, GH, MO, US, POM, CAS, RM, UT, UTC, and others).

ADDITIONAL SPECIMENS: **Utah.** Uintah County, Crack of rock cliff, Brush Creek Gorge, at ca. 1980 m, 11 August 1935, *E. H. Graham 10009* (CM).

Plants 2.5–6 dm tall; stems copiously to rather sparingly glandular and with adhering sand grains here and there throughout; leaves mainly basal, 4–24 cm long, biternate, rather copiously villous-glandular, green on both sides but paler beneath; flowers

usually 2–6 or more, nodding, somewhat longer than broad; sepals horizontally spreading, 11–14 mm long, red-fuchsia; petals with spurs colored like the sepals, the blades clear yellow, 5–6 mm long; spurs 18–21 mm long; stamens exceeding the blades by 9–13 mm; follicles unknown. Sandy soil along drip line below weeping, hanging garden cliffs of Weber sandstone, with *Calamagrostis scopulorum,* at ca. 2320 m, in deep, shaded canyons in the eastern Uinta Mts., Uintah County; endemic.

This is another in a series of variants within the genus *Aquilegia* in Utah. Early treatments of the genus recognized only *A. micrantha* as being glandular overall, and all specimens encountered that were so clad were placed within that entity. Such placement ignores other features of flowers, overall nature of the plants, and phytogeography. The attempt in recent years has been to place the glandular plants with apparent nearest congeners. The present instance recognizes the similarities and differences of this plant, with its syndrome of features unmatched by the other taxa. This plant simulates *A. micrantha* in being glandular throughout, but the flowers are startlingly red-fuchsia contrasting with yellow, not white to pale blue or pinkish. Additionally they are longer than broad. From *A. formosa,* which has similar though more scarlet than red-fuchsia flowers, it differs in being glandular overall and in having flowers longer than broad. It differs from the glandular, var. *fosteri,* of that species in having shorter sepals, shorter petals, and shorter spurs, and from *A. flavescens* var. *rubucundula* in the darker flowers, larger size of the plant, and flowers longer than broad. The species was first discovered in 1935 by E. H. Graham (1937) when he was involved with his classic investigation of the botany of the Uinta Basin. The species is named in honor of his amazing contribution.

RHAMNACEAE

**Ceanothus greggi** Gray var. **franklinii** Welsh, *var. nov.* Affinis var. *vestito* (Greene) McMinn sed in staturis inferioribus et petalis plerumque cyaneis differt (Plate I: Figure 20).

TYPE: USA. **Utah.** San Juan County, T41S, R17E, S12, Muley Point, at 1891 m, rimrock, pinyon-juniper community, Cedar Mesa Sandstone, 8 June 1983, *S. L., B. T., and M. L. Welsh 22244* (HOLOTYPE BRY!; three isotypes distributed previously as *C. greggii*).

ADDITIONAL SPECIMENS: **Utah.** Grand County, ca. 7 mi. E of Moab, N slope of

Mill Creek, 26 April 1986, *B. Franklin 2857*; small mesa between Onion Creek and Fischer Mesa, 17 May 1985, *B. Franklin 1593*. San Juan County: Young's Canyon, tributary to Dark Canyon, ca. 2 mi. upstream from canyon mouth, 27 August 1977, *B. Mikus 610*; SE end of Spanish Valley, 26 April 1986, *B. Franklin 2842* (all BRY!).

This low ceanothus is often a rimrock plant in pinyon-juniper and associated shrublands in Grand and San Juan counties. It seldom surpasses 5 dm in height and typically has flowers that are blue or fade that color. The plants are isolated geographically from the remainder of the species in Utah. The following key will allow segregation of the Utah materials.

1. Shrubs 2–5 dm tall, intricately branched; flowers typically blue or fading blue; plants of the Colorado drainage system *C. greggii* var. *franklinii*
– Shrubs mainly 10–20 dm tall, not especially intricately branched; flowers typically white and drying white; plants of the Virgin drainage system and environs *C. greggii* var. *greggii*

Var. **franklinii** Welsh Pinyon-juniper, blackbrush, shunkbush, and serviceberry communities at 1645 to 1895 m in Grand and San Juan counties (type from Muley Point, *S. L., B. T., and M. L. Welsh 22244,* BRY!); endemic.

The plants occur as scattered shrubs over a wide area in Grand and San Juan counties. There is a specimen at BRY! (*Nixon 16274,* 1985) with label data indicating that it was taken in Garfield County northwest of Escalante at North Creek Reservoirs between Barker Reservoir and Flat Lake in an aspen-spruce-fir community. The locality should be revisited and the collection verified.

Var. **vestitus** (Greene) McMinn [*C. vestisus* Greene]. Mixed desert shrub, pinyon-juniper, and mountain brush communities at 1220 to 2870 m in Iron and Washington counties; Nevada, California, Arizona, New Mexico; Texas, and Mexico.

Plants from Washington County are typically much taller (1–2 m). The species is grown as a specimen plant on the campus of the University of Utah in Salt Lake City (*Labrum 4,* 1970 BRY!).

## SCROPHULARIACEAE

**Penstemon franklinii** Welsh, *sp. nov.* A *Penstemon pinorum* L. & J. Shultz in habitu compacto, foliis caulini latioribus, inter-

nodiis brevioribus, floribus majoribus et antheris longioribus differt (Plate I: Figure 21).

TYPE: USA. **Utah.** Iron County, T34S, R11W, NW/SE S8, ca. 10 km due NW of Enoch, N end Cedar Valley, three-awn, needle grass, matchweed, black sagebrush community at 1655 m, 27 May 1993, *M. A. Franklin & L. Armstrong 7662* (HOLOTYPE BRY!; ISOTYPES NY, GH, MO, US, POM, CAS, RM, UT, UTC).

ADDITIONAL SPECIMENS: **Utah.** Iron County, ca. 15 km WNW of Summit, N end Cedar Valley, 26 May 1993, *M. A. Franklin & L. Armstrong 7660*; ca. 5 km W of Rush Lake, 27 May 1993, *L. Armstrong & M. A. Franklin 429*; ca. 10 km due NW of Enoch, N end of Cedar Valley, 28 May 1993, *M. A. Franklin 429*; ca. 10 km due NW of Enoch, N end of Cedar Valley, 28 May 1993, *M. A. Franklin 7666* (all BRY!, with numerous duplicates to be exchanged).

Perennial herb from a branching caudex; stems 6–25 cm tall, compact, the lower two nodes less than one-third the plant height, puberulent almost throughout, becoming glandular-hirsute above; leaves 1.2–6.5 cm long, 2–8 mm wide, variously all entire to all toothed, the uppermost cauline and bracteate leaves commonly toothed, the basal ones long-attenuate to a petiolar base, the blades glabrous on both sides or puberulent along the middle above, the cauline leaves and bracts lance-attenuate, more or less clasping; inflorescence conspicuously glandular-hirsute, lax or congested, not secund; verticillasters 3–7, the cymes 3- to 5-flowered; calyx 4.8–7.5 mm long, glandular-hirsuite to -pilose, the lobes lanceolate to elliptic, cyaneus apically; corolla 14–22 mm long, moderately ampliate, blue to blue-lavender, the palate yellow-bearded, with purple guidelines; staminode included or only slightly exserted, bearded with flattened golden yellow hairs for half its length; anthers glabrous, 1.6–1.8 mm long, the sacs parallel, dehiscing the full length and across the connective, not explanate. Three-awn, needlegrass, matchweed, and black sagebrush communities at 1650 to 1800 m in Cedar Valley, Iron County; endemic.

*Penstemon franklinii* belongs to Section Cristati, a group of closely allied species, many of them rather narrow endemics of desert regions extending from Colorado to Idaho, Oregon, Nevada, and California. This species has as its nearest ally, both morphologically and geographically, the pinyon penstemon, *P. pinorum,* a plant from nearby to the south in Iron County. Similar occurrences of nearly associated geographical elements are to be found in *P. concinnus* Keck, *P. nanus* Keck, and *P. dolius,* all of which occur in west desert valleys of Utah. Each of those differ

in about the same manner and degree from each other as *P. franklinii* does from *P. pinorum*. *P. pinorum* has all leaves more or less strongly and sharply toothed, the lower two internodes make up one-third to one-half of the plant height, the cauline leaves are linear and rather abruptly widening to clasping bases, the purple-blue corollas are 10–15 mm long, and the anthers 1–1.2 mm long. By contrast, *P. franklinii* has leaves variably toothed to entire, the lower two internodes are not elongated, making up less than a third of the plant height, the cauline leaves are lance-attenuate and rather gradually broadened to the clasping base, the blue corollas are 14–22 mm long, and the anthers 1.6–1.8 mm long.

The species is named after M. A. (Ben) Franklin, co-discoverer of the species and co-collector of the type specimen. Mr. Franklin is one of the outstanding field workers in botany today.

**Penstemon humilis** Nutt var. **desereticus** Welsh, *var. nov.* Similis *P. humilis* var. *humilis* in habitis sed in floribus majoribus et corolla lobis brevioribus et tubis latioribus differt (Plate I: Figure 22).

TYPE: USA. **Utah.** Juab County, West flank of the Deep Creek Mountains, Rock Spring Canyon, ca. 7 mi. SSE of Ibapah, T10S, R18W, S19, pinyon-juniper woodland, siliceous gravel, 8 June 1978, *S. Welsh, R. Foster, and J. Henriod 16858* (HOLOTYPE BRY!; six isotypes distributed previously as *P. humilis* Nutt.).

ADDITIONAL SPECIMENS: USA. **Utah.** Beaver County, Mountain Home Range, 28.5 mi. S of Garrison, 21 June 1983, *S. Goodrich 18550*; Wah Wah Mountains, Pine Grove Canyon, 27 May 1978, *S. Goodrich & L. Hart 11198*; Indian Peak Range, 16 June 1978, *K. Ostler & D. Anderson 1410*; Indian Peak Range, ca. 7 mi. S of Sawtooth Peak, 26 May 1976, *S. Welsh, K. Taylor, and F. Peabody 13295*. Iron County, Indian Peak Range, Arrowhead Pass, 16 June 1973, *K. Ostler & D. Anderson 1402*. Juab County, Deep Creek Range, Thom's Canyon, 18 June 1977, *A. Holmgren and L. & J. Shultz 16471*; Deep Creek Mountains, T11S, R18W, S10, pinyon-grass community, 8 June 1978, *S. Welsh, R. Foster, and J. Henriod 16919*. Millard County, Tunnel Springs Range, Desert Experimental Range, 23 June 1983, *S. Goodrich 18703*; 15 June 1982, *S. Goodrich 16919*; all BRY!.

Pinyon-juniper and mountain mahogany communities, on dolomite, limestone, and siliceous outcrops and gravels, at 2135 to 2680 m in Beaver, Iron, Juab, Millard, and Tooele counties; a Great Basin (i.e., Deseret) endemic.

AGAVACEAE

**Yucca vespertina** (McKelvey) Welsh [based on: *Yucca baccata* Torr. in Emory var. *vespertina* McKelvey, Yuccas of the SW U.S. 1: 45. 1938].

This conspicuous component of the Mohave Desert flora stands in marked contrast to its mesic counterpart, *Y. baccata.* The long, markedly glaucous, stiff, strongly involute or almost folded leaves, flowers suffused in bud with red-brown or red-purple, and colonial habitat set the Mohave yucca apart from the baccate yucca in about the same manner and degree that other species of yucca are distinguished. The plants are remarkable xerophytes, surviving on the very low rainfall and high temperatures of the low elevation deserts. This strongly glaucous phase grows with creosote bush, Joshua tree, blackbrush, bursage, and other warm desert shrubs. By contrast the baccate yucca has green, only relatively stiff, merely concave leaves, wine-colored flower buds, and tend not to be markedly colonial. It is at least moderately mesophytic, occurring at moderate elevations in the pinyon-juniper community and above. The recognition of *Y. vespertina* at specific level seems long overdue.

LILIACEAE

Specimens of an unusual onion, identified as *A. geyeri,* were noted in *A Utah Flora* (Welsh et al., 1987, p. 803). The collection consisted of a set of 10 duplicates from the northeast margin of the Abajo Mountains in San Juan County. During the interim six additional collections from various parts of the Abajo Mountains demonstrate that the initial specimens were not merely an aberration. They are, therefore, described as follows:

**Allium geyeri** Wats. var. **chatterleyi** Welsh, *var. nov.* Similis *A. geyeri* var. *geyeri* in propriate generaliter sed in bulbis tunicae marcescentibus multistratis et longioribus differt (Plate I: Figure 23).

TYPE: USA. **Utah.** San Juan County, T32S, R22E, S27, head of Indian Creek Canyon, at ca. 2015 m in pinyon-juniper community on Navajo Sandstone, 2 August 1983, *S. L. Welsh, B. T. Welsh, & M. Chatterley 22371* (HOLOTYPE BRY!; isotypes, nine distributed previously as *Allium*).

ADDITIONAL SPECIMENS: **Utah.** San Juan County, Abajo Mts., Cliff Dweller's Pasture, 27 June 1984, *J. S. Tuhy 1519*; Horse Mountain, 27 June 1991, *M. A. Franklin & B. Thompson 7228*; Trough Canyon, 9 July 1992, *M. Ben Franklin 7559*; Little Dry Mesa, 28 June 1990, *M. A. Franklin & B. Thompson 7235*; Tuerto Canyon, 12 July 1990, *M. A. Franklin 7275*; Chippean Ridge, 11 July 1990, *M.A. Franklin 7275*; all BRY!.

Chatterley's onion. The variety is named in honor of Matthew Chatterley, co-collector of the type. The species complex is described below:

*Allium geyeri* Wats. Bulbs .7–2 cm thick and about as long or longer, ovoid, buried 1–8 cm below ground, the scales fibrous-reticulate, more or less persistent and extending from the root crown to 11 cm up the flowering stem; leaves 2 or 3 per scape, shorter than the scape, 1–5 mm wide, concave-convex; scapes 15–50 cm tall (above ground); spathaceous bracts 2 or 3, mostly 1-veined; umbels 5- to 37-flowered, the pedicels straight or curved; perianth pink or white, 6–10 mm long, the segments subequal, with tips more or less recurved, often replaced by bulblets; stamens included; capsule inconspicuously low-crested.

1. Marcescent bulb scales few layered, extending 2–4 cm up the flowering stem; plants of broad distribution *A. geyeri* var. *geyeri*
– Marcescent bulb scales many layered, extending 4.5–11 cm up the flowering stem base; plants from the Abajo Mts. *A. geyeri* var. *chatterleyi*

Var. *chatterleyi* Welsh Pinyon-juniper, ponderosa pine-manzanita, and mountain mahogany communities in San Juan County (type from head of Indian Creek, *Welsh et al. 22371,* 1983, HOLOTYPE BRY!); endemic.

Var. *geyeri* Pinyon-juniper, ponderosa pine, sagebrush, aspen, grass-forb, and spruce-fir communities, typically in moist sites, at 2105 to 3540 m in Cache, Daggett, Duchesne, Emery, Garfield, Rich, San Juan (La Sal Mts.), Summit, Uintah, and Wasatch counties; British Columbia and Alberta, south to Oregon, Nevada, Arizona, New Mexico, and Texas.

## ORCHIDACEAE

A decade ago, Sheviak (1984) named a new orchid from Colorado, whose distribution includes portions of Utah and Nevada,

in addition to Colorado. That taxon, *Spiranthes diluvialis,* has received considerable attention during the interim. It was finally listed by the U.S. Fish and Wildlife Service as a threatened species under stipulations of the Endangered Species Act of 1973, as amended. Previously and subsequently the same author has named additional species in the genus (Sheviak, 1973, 1989, 1990). Most of these fit within the concept of *S. romanzoffiana sensu lato,* which had been reported in the literature as having more than one base chromosome number. Those different base chromosome numbers have been used by Sheviak as evidence to support the taxa treated. Careful examination of the several sheets now available for study from Utah have demonstrated that most specimens in the *romanzoffiana* complex can be logically and reasonably segregated into two stacks. There are specimens, however, that are difficult to place into one or the other category. Because of the intermediacy of those specimens and the problematic utilization of features of the lip in dried specimens, it is here proposed that *S. diluvialis* be treated at varietal level.

**Spiranthes romanzoffiana** Cham. var. **diluvialis** (Sheviak) Welsh, *comb. nov.* [based on: *Spiranthes diluvialis* Sheviak, Brittonia 36: 11. 1984].

The species and its varieties in Utah are described below:

*Spiranthes romanzoffiana* Cham. Plant erect, stout to slender, glabrous below, pubescent to almost glabrous above, .8–6 dm tall; roots fleshy, fasciculate; basal leaves 2–4, 3–32 cm long, 2–13 (15) mm wide, linear-oblanceolate, cauline ones 2–6, greatly reduced and finally bracteate upward; floral bracts ovate- to lance-attenuate; flowers creamy white, 7.5–15 mm long; sepals and petals connivent and forming a hood over the column; sepals lanceolate, 7.5–15 mm long, 3–4 mm wide, the lateral somewhat falcate; petals triangular-attenuate, obtuse, 7.5–15 mm long, 1–2.5 mm wide; lip oblong to pandurate, 7.5–12 mm long, ca. 5 mm wide, constricted at or above the middle, the apex entire or erose, dilated and without papillae, the basal callosities minute to prominent; $2n = 60, 74$.

1. Petals free for (3.5) 4.5–6.5 mm; rachis of inflorescence with at least some hairs more than .2 mm long; plants of middle and lower elevations *S. romanzoffiana* var. *diluvialis*
– Petals free for 2–3.5 mm; rachis of inflorescence glabrous or

with very short glandular hairs, mainly less than .1 mm long; plants of middle to upper elevations *S. romanzoffiana* var. *romanzoffiana*

Var. *diluvialis* (Sheviak) Welsh Intermountain ladies-tresses. Wet meadows, stream banks, abandoned oxbow meanders, marshes, and raised bogs at 1370 to 2085 m in Daggett, Duchesne, Garfield, Salt Lake, Tooele, Uintah, Utah, Wayne, and Weber counties; Nevada and Colorado; $2n = 74$.

Specimens of this entity vary from clearly identifiable to questionably identifiable. There is no single character or combination of characteristics that will allow for determination of all specimens and, counting of chromosomes in not a practical option. The diagnostic criteria overlap, as do the sizes of the plants and the elevational ranges. Shape of the lip and the presence and degree of development of callosities at the lip base are difficult to discern in dried, pressed material. At least some of the principal habitat is along lake shores and waterways that are privately owned, places not readily available to collectors; certainly it is more abundant than the few specimens extant in herbaria seem to indicate.

Var. *romanzoffiana* Bogs to open woods in lodgepole pine, aspen, spruce-fir, and alpine tundra communities at 1735 to 3310 m in Daggett, Duchesne, Juab, Salt Lake, Summit, Uintah, Utah, Wasatch, and Washington counties; Alaska to Newfoundland and southward to California, Arizona, New Mexico, Michigan, and Pennsylvania; $2n = 60$.

Plants of this variety thrive in a heavily grazed wet meadow pasture in Summit County, flowering brightly in a field grazed as close as a lawn. Thus, grazing by itself does not appear to constitute a serious threat to this species.

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RHODORA, Vol. 95, No. 883/884, pp. 422–424, 1993

## NEW ENGLAND NOTE

# SOME NEW RECORDS FOR ALGAE IN SOUTHEASTERN MASSACHUSETTS

L. C. Colt, Jr., S. M. Baskinger, M. O. Fontaine,
T. W. Howie, K. Richards and K. A. Simmons

Field work in North Dartmouth, MA, on and near the campus of the University of Massachusetts Dartmouth yielded fresh water algae not previously reported for Bristol County, and one new record for Massachusetts. Woelkerling (1973), Prescott (1982), and Prescott et al. (1981, 1982) were used for identification, and distribution records were checked using the New England Algal Data Bank (NEADB, Colt, 1993), in the library of the Marine Biological Laboratory, Woods Hole, MA. Previous collections are listed (in parentheses) by county in Massachusetts as reported in the NEADB. Page references are from a draft manuscript of the NEADB in the possession of the senior author. Length (L), width (W) and isthmus (I) measurements are in microns.

### DESMIDIACEAE

1. **Micrasterias tetraptera** W. et G. S. West. L 116, W 102, I 21. Collected in a low field drainage from a wooded area, the latter dominated by Atlantic Coast White Cedar (*Chamaecyparis thyoides* (L.) BSP) and Sphagnum (*Sphagnum* sp.) moss. The site is approximately 125 meters west of Ring Road, and approximately 300 meters north of the Cedar Dell Housing complex driveway on the UMD campus. (New state record. Previously only reported from New Hampshire. NEADB, p. 531.)
2. **Euastrum oblongum** (Grev.) Ralfs. L 124.2, W 54, I 40. In same drainage as No. 1. (Barnstable, Dukes, Hampshire, Nantucket & Worcester Counties, MA. NEADB, p. 362.)
3. **Staurastrum alternans** Breb. L 31, W 28, I 10. In roadside ditch adjacent to same drainage as No. 1. (Barnstable, Hampshire & Worcester Counties, MA. NEADB, p. 829.)
4. **Staurastrum cyrtocerum** (Breb.) Ralfs. L 36, W 34, I 10. In same drainage as No. 1. (Barnstable, Hampshire & Worcester Counties, MA. NEADB, p. 837.)

5. **Staurastrum muricatum** Breb. L 46, W 41, I 18. In same drainage as No. 1. (Hampshire & Worcester Counties, MA. NEADB, p. 850.)
6. **Staurastrum punctulatum** Breb. L 38, W 36, I 13. In same drainage as No. 1. (Barnstable, Dukes, Essex, Hampshire, Plymouth & Worcester Counties, MA. NEADB, p. 855.)
7. **Arthrodesmus extensus** (Ehren.) Ralfs var. **longispinus** (W. et G. S. West) Bicudo. L 18, W 10, I 8. In roadside ditch adjacent to and from the same drainage as No. 1. (Previously reported for MA, with no county named. NEADB, p. 56.)
8. **Euastrum binale** (Turp.) Ralfs var. **gutwinski** (Schm.) Krieger. L 23, W 18, I 5. In same drainage as No. 1. (Barnstable County, MA. NEADB, p. 354.)
9. **Draparnaldia glomerata** (Vauch.) C. A. Agardh. Collected from concrete discharge trough from pond adjacent to entrance to UMD campus. (Middlesex & Worcester Counties, MA. NEADB, p. 319.)
10. **Staurastrum bieneanum** Raben. var. **ellipticum** Wille. L 15, W 30, I 5. Collected from a roadside drainage ditch on the west side of Route 140, approximately 400 meters north of the New Bedford town line, in Freetown, MA. (Hampshire & Worcester Counties, MA. NEADB, p. 833.)
11. **Cosmarium polygonum** (Naeg.) Archer. L. 13, W 13, I 5. In same ditch as No. 10. (Dukes County, and an unnamed site in western (?) MA. NEADB, p. 249.)

### ACROCHAETIACEAE

12. **Audouinella purpurea** (Lightf.) Woelkerling. Collected in a brook below the intersection of Drift Road and State Route 88 from submerged sides of the west end of a drainage culvert pipe which passes under Route 88 in Westport approximately ¼ mile north of where Route 88 crosses the East Branch of the Westport River. (Barnstable, Dukes, Essex & Plymouth Counties, MA. NEADB, p 71.)

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# NEW ENGLAND NOTE

## *CAREX PRAEGRACILIS* W. BOOTT (CYPERACEAE) NEW TO NEW ENGLAND

A. A. Reznicek and M. J. Oldham

*Carex praegracilis* is a widespread, western salt tolerant species that has been spreading rapidly along highways in the eastern United States. Its distinguishing characteristics and local spread have been documented in Ontario by Reznicek, Catling, and McKay (1976) and Brunton and Catling (1982) and in Ohio by Cusick (1984). Reznicek and Catling (1987) mapped the recent, rapid spread of the species on a North American wide scale, and reported occurrences as close to New England as easternmost New York. They noted that "The species has suddenly become common well to the east, reaching almost to the New England States." Up to now, however, *C. praegracilis* has not been reported from New England (Seymour, 1982).

Clearly, the spread of *Carex praegracilis* into New England was inevitable. In 1992, both of us had the opportunity to travel in New England, and we found *C. praegracilis* at three sites, two in Vermont and one in Maine, as documented by the specimens cited below:

**MAINE.** Penobscot Co.: Bangor, Hwy. 95, 2.9 km W of exit to Hwy. 395, scattered clumps for 10+ km in centre median, *Oldham 13794*, June 12, 1992 (MAINE, MICH, NEBC, herb. M. J. Oldham, herb. M. Blondeau).

**VERMONT.** Chittenden Co.: E side I-89, 4.9 mi. N of interchange with Hwy. 2 & 117, outskirts of Winooski, upper edge of moist ditch in median strip, *Reznicek 9118 & Reznicek,* July 11, 1992 (DAO, MICH, NEBC, TAES, VPI, VT, herb. C. T. Bryson, herb. V. McNeilus); Washington Co.: 10 mi. N of Montpelier, Hwy. 89, scattered patches in centre median for several miles, *Oldham 13789,* June 11, 1992 (DAO, MICH, NEBC, VT).

The Maine collection is the farthest northeast that the species has been found to date. The occurrence of *Carex praegracilis* along I-89 and I-95 is very localized as yet, with only the three sites observed. No other occurrences were seen along any of the other highways travelled. Nevertheless, based on the behavior of the species elsewhere in its newly occupied range, *C. praegracilis* can

be expected to continue to spread. *Carex praegracilis* occurs especially frequently on multi-lane expressways; so much so that it has earned the common names "tollway sedge" (Swink and Wilhelm, 1979) or "freeway sedge" (Brunton and Catling, 1982; Gleason and Cronquist, 1991). We venture to predict that *C. praegracilis* will, in time, be found along every major expressway in New England and become a significant component of highway verge vegetation.

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*Vol. 95, No. 882, including pages 85–196, was issued October 20, 1993.*

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